Developing methods for calculating individuality in moose movement behavior from remotely-collected location data

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Abstract

A rapidly-expanding literature on behavioral syndromes has revealed animal "personalities," or behavioral differences that are consistent through time and across contexts, in a wide range of taxa. Despite evidence of behavioral syndromes in many species, little has been done to consider the importance of this behavioral variation for management plans, which are developed based on averages. One problem is the intractability of conducting in-field behavioral assays on many managed wildlife populations. We studied the movement behavior of 35 moose (*Alces alces*) in northeastern Minnesota to determine if behavioral syndromes can be detected remotely in this population. If remote detection is possible, then behavioral variation could be assessed without the challenges associated with in-field assays. Location data were used to calculate various movement-related behavioral metrics, and landcover and terrain maps were used to quantify features of the environment. Behavioral metrics were used in a cluster analysis to look for patterns within and among individuals, and variation was also related to environmental variables. The optimal clustering approach included two metrics (daily path length and net daily displacement) to define five clusters ($R^2 = 0.94$). When observations were plotted by NMDS, there was no distinct separation among the cluster groups. Clusters were not explained by the measured environmental variables, and there was a low rate of reclassification for individuals across multiple years. The methods were sufficient to produce general patterns consistent with what is known about moose behavior (e.g., reduced movement in winter, high use of forested cover types, and increased preference for aquatic features in summer). Overall, when using this approach it was unclear which variables were informative and appropriate for inclusion in clustering. The implications of behavioral variation for management remains an important subject, and we recommend conducting an in-field behavioral assay and then using the resulting behavioral scores to inform a multivariate analysis of movement-related metrics. This approach would help to determine which, if any, of the remotely-calculated metrics are able to identify behaviorally-defined groups.

Table of Contents

List of Tables and Boxes

List of Figures

Key to Variables and their Abbreviations

Animal ID: Animal identification number; unique to an individual. There are 35 animal IDs in the utilized dataset.

sex: Male (M) or female (F). Dataset includes 28 females and seven males.

season: Winter (1 Dec-31 Mar) or summer (15 Jun-15 Sep).

year: Year during which the data were collected; corresponds to the season, not the date. E.g., 15 February 2010 is part of winter 2009. Dataset spans winter 2009-winter 2014.

severity: Seasonal severity indices were created based on known heat stress thresholds of moose. Severity values were normalized (0-1) by season, since summer and winter had different indices and different ranges of values.

SARI: measure of terrain ruggedness based on slope and aspect, applied within a buffer (circle with radius of 2 km on centroid of home range) or within a home range (95% isopleth of biased random bridge utilization distribution kernel).

$$SARI = \frac{(standard\ deviation\ of\ slope) * (variety\ of\ aspect)}{(standard\ deviation\ of\ slope) + (variety\ of\ aspect)}$$

Variety of aspect: the number of "ups" and "downs" along a transect (Nellemann and Fry 1995).

V: Average step velocity (i.e., movement rate), in meters per hour. A "step" is a pair of location coordinates and the space and time between them.

D: Diffusion parameter (m^2/second), calculated via maximum likelihood method. Unique to individual for each season-year.

DPL: Average daily path length, in meters.

disp: Average net daily displacement, in meters.

anglescore: A score of 1-5 assigned to the empirical distribution of turning angles, to quantify differences in directional patterns of travel; based on whether the distribution had one or two strong means and whether there was high or low concentration around the mean(s), or if the distribution was mostly uniform (Box 2).

kappa direction: binary variable based on whether the individual's turning behavior was more concentrated in the forward direction (angles between -0.5π, 0, and 0.5π; assigned "1") or the backward direction (angles between $\pm 0.5\pi$ and $\pm\pi$; assigned "0").

hr95: area of 95% isopleth of biased random bridge utilization distribution kernel, in km^2.

SSmean: Volume of intersection (kernel overlap) between home range of an individual and other collared individuals during a given season-year. Reported as a mean volume.

fidelityVI: Volume of intersection (kernel overlap) between home ranges of an individual from one year to the next. Summer and winter assessed independently. Calculated between subsequent years in all but two cases. Values not available for all individuals.

diff###: A measure of resource selection:

$diff\#\#\# = n\#\#\# - b\#\#\#$, where

is a three-digit code for a land cover type,

n### is the proportion of kernel space attributed to that cover type, and

b### is the proportion of that cover type within the buffer.

Values < 0 mean that the animal is using that cover type proportionally less than its availability in the general area; values > 0 indicate that the animal is using cover type proportionally more than its availability.

Code	*Cover Type*
100	Developed/Urban
101	Emergent Wetlands
102	Forested Wetlands
103	Open Water
104	Extraction
105	Conifer Forest
106	Deciduous Forest
107	Mixed Forest
108	Regenerated Forest
109	Grassland
110	Hay & Pasture
111	Row Crops

Extended Background

The concept of an "average" is widespread and used often in daily life (e.g., on average, it takes me 30 minutes to get to work) as well as in nearly every academic discipline, including animal behavior and ecology. Our use of the average has expanded a great deal from its very functional origin in astronomy. Starting in the second century BC, observers needed to reconcile differing repeated measures of astronomical phenomena (Stahl 2006). Early methods included favoring the middle range of values or simply selecting the most convenient or desirable value. By the end of the 1500s AD, Danish astronomer Tycho Brahe included the treatment of repeated measurements in his rigorous methodology, although he did not specify his methods of calculation; astronomers continued to utilize means and medians in dealing with measurement errors (Stahl 2006).

This astronomical "method of averages" was first applied to other fields in the 1830s when the Belgian revolution crushed the career trajectory of young mathematician Adolphe Quételet (Rose 2016). The turmoil induced a newfound concern in social behavior, and he decided to apply his scientific methods to studying humans (Rose 2016, Porter 1986). Since then, averages have pervaded nearly every facet of life imaginable, from the use of average bodies for clothing sizes to evaluating work performance to the structuring of entire educational systems (Rose 2016).

The averagarian method, which sacrifices the truth of the particular in the search for the universal, is also called the "aggregate approach:" data are grouped, and then analyzed (Todd et al. 2013). Despite its popularity and pervasiveness, tabulating averages without giving serious thought to the intended unit of analysis can yield misleading conclusions. Since at least the 1950s, scholars have been describing significantly undesirable issues associated with using this approach (e.g., Robinson 1950). Specifically, the results of computations on group means or proportions are not perfectly representative of the conclusions that would result from computing at the level of the individual; Selvin (1958) called this phenomenon an "ecological fallacy." This designation stems from methods of *ecological correlation*, in which the statistical object

is a group (Robinson 1950). Ecological correlations contrast with *individual correlation*, in which the object is an indivisible unit, and are appropriately used when individual-level data are not available and such correlations cannot be calculated (Robinson 1950). Thus, ecological fallacy is a general occurrence not at all restricted to the scientific field of ecology, and it is observed in disciplines ranging from archaeology to physics, politics, and population genetics (Levin 1992).

Robinson (1950) showed that the theoretical conditions that are necessary for ecological and individual correlations to be equivalent are never satisfied in a realistic dataset. Specifically, the average within-group individual correlation is realistically never less than the total individual correlation (Robinson 1950). Based on this information, he argued that the results from ecological correlations cannot simply be substituted for individual correlations.

In fact, the average value or association calculated for a group need not accurately represent any single individual within that group; and often times it does not (Rose et al. 2013, Estes 1956). In the 1940s the United States Air Force was suffering from high rates of "pilot error" and associated fatalities (Rose 2016). Fighter plane cockpits had been designed based on the averaged body size measurements of hundreds of male pilots in 1926; thinking that their average might be outdated, in 1950 the Air Force took new measurements of 140 body dimensions on 4063 pilots to update their "average pilot" (Rose 2016, Randall et al. 1946, Hertzberg et al. 1954). A skeptical new lieutenant, Gilbert Daniels, did some extra calculations. He calculated averages for the ten most relevant body dimensions, and defined any individual whose measurements were in the middle 30% of the range as being "average"; out of 4,063 pilots, not one of them was average in all ten dimensions, and less than 3.5% were average in just three of the ten dimensions (Daniels 1952, Rose 2016). Once cockpits were re-designed to be adjustable to the individual body, the Air Force observed far fewer incidences of pilot error (Rose 2016).

Issues of aggregate error and ecological fallacy have been considered in several disciplines for decades. In his 1992 MacArthur Award lecture, "The Problem of Pattern and Scale in Ecology," Simon A. Levin alluded to the effects of ecological fallacy in ecology. Ecologists work to decipher the mechanisms that lead to observable patterns, but

these patterns vary with different spatial, temporal, and organizational scales (Levin 1992). Can we understand processes at an individual level if we are observing the population level? Previous methodological scrutiny suggests that perhaps we cannot. While some scales of observation are limited by uncontrollable factors such as perception and technology, others are limited by choice (Levin 1992, Wiens 1989). Whenever choice is involved, a decision must be made regarding whether or not it is acceptable to focus on coarse patterns of larger units—groups, areas, or time periods—at the expense of understanding individuality and variability.

Introduction

Individuality is a concept that is typically dismissed in wildlife management, where the goal is to manage populations rather than distinct animals (Krausman and Cain 2013). The typical approach, in which data are *aggregated* and then *analyzed*, is used because the population is the unit of analysis; averages yield information about groups, which is useful for comparing groups, and populations are indeed groups. However, this aggregation can lead to incorrect interpretations of the data. For example, averaging individual responses when there is sufficient variation in the population will result in a population-level trend that does not match those of the individuals (Bissonette and O'Neill 1979). This is an issue of scale, known as *aggregation error*, which occurs when measurements taken at fine resolutions are extrapolated to a larger scale or unit of interest (Bissonette 2013).

For many questions, analyzing general population patterns is sufficient. For example, measurements of hair cortisol concentrations and home range areas of individual caribou were *aggregated* by population and then *analyzed* to identify regression correlations between cortisol and home range size, and *the differences among five populations* (Ewacha et al. 2017). However, while the goal of wildlife management is to maintain population units rather than specific individuals, it is important to recognize that a population is composed of individuals, which are unlikely to be all (or even mostly) average. The patterns of a population emerge from the combined behavior of individual

units, and correctly understanding the mechanisms underlying population patterns is central to developing effective management policies (Levin 1992).

There is a rapidly-expanding literature on the presence of behavioral syndromes (i.e., animal "personalities") in a vast range of taxa, from spiders (e.g., Riechert and Hedrick 1993) to fish (e.g., Cote et al. 2010) to elk (e.g., Found and St. Clair 2016) and even bacteria (e.g., De Winter et al. 2014). Behavioral syndromes are phenomena in which there are differences in behavior within a population or a species that are consistent within an individual through time and across contexts (Sih et al. 2004). A behavioral syndrome may be viewed as a gradient of a particular behavioral characteristic, for example boldness, and an individual's position on this gradient is called a behavioral "type." When groups of individuals fall on opposite ends of the spectrum they may be categorized by their distinct temperaments, such as "bold" or "shy." This new dimension of animal behavior can more accurately inform questions relating to how wildlife species use and interact with landscapes, and is nicely reviewed by Spiegel et al. (2017).

Despite the mounting support for behavioral syndromes in many species, little is being done to consider whether behavioral types can be useful in designing conservation and management plans. One convincing example, a recent study of habituated populations of elk in Canada, identified distinct behavioral types that differed in migration behavior (Found and St. Clair 2016). The authors measured seven different behavioral metrics to assign each individual a score ranging from shy to bold. The shyer half of the population was three times more likely to migrate while the bolder half was more likely to stay as year-round residents (Found and St. Clair 2016). This study was focused on management concerns related to the impacts of human-wildlife interactions, and the consequences of habituation for both natural movement patterns as well as public safety concerns. The results of this study suggest that it may be important to rethink the traditional representation of populations, and particularly ungulate populations, as homogeneous groups of individuals.

Studies on behavioral syndromes utilize behavioral assays that are conducted in-person, either in the field or in the lab (Sih and Bell 2008). For example, in a lab setting crayfish were assayed on their intraspecific aggression, willingness to forage on novel

prey and to forage under risk of predation, and their initial reaction to putative predation (Pintor et al. 2008). In the field, elk have been evaluated based on positioning and leading behavior within their herd, flight response distances, responses to novel sounds and objects, and time spent vigilant (Found and St. Clair 2016). However, many factors make in-person assays intractable for some taxa, perhaps especially those in the greatest need of improved management policies. A species' abundance on the landscape and the habitats in which it is found can be prohibitive to gathering a large enough sample size, while limited funding or regulatory legislation might make such endeavors impossible.

Rapid technological advances in the 21st century have improved methods of remote data collection for various taxa. From GPS telemetry to bio-logging, the generation of large remote datasets comes with many opportunities as well as challenges (Hebblewhite and Haydon 2010). Animal-borne GPS collars can record and send the specific locations of individuals at frequent and mostly regular time intervals, allowing them to be tracked across the landscape as they conduct normal activities. This technology has yielded finer-scale information on wildlife habitat requirements for different activities, species distributions, and mechanisms of migration, among other benefits (Hebblewhite and Haydon 2010). Biotelemetry devices include bio-loggers that can record heart rate, body temperature, metabolic rate, depth via pressure sensors, and more (Cooke et al. 2004). Thus, it is possible to collect a wide range of physiological and behavioral data remotely, after an initial capture and outfitting of the animals.

Movement (i.e., changes in an individual's spatial location through time; Nathan et al. 2008) is one fundamental behavior type that can be affected by, and can affect, myriad internal and external factors. Studying the behavioral and environmental context within which organisms move can elucidate linkages between landscape characteristics and population demographics, which is important for management. A framework was put forth by Nathan et al. (2008) to unify studies of movement ecology, and behavioral type can influence several of their defined components of movement (Spiegel et al. 2017). For example, temperament can affect what environmental factors an individual experiences, what situations motivate them to actually move, and whither they move. Behavioral syndromes may also be linked to physical traits that affect movement (e.g., metabolism and hormones; Spiegel et al. 2017, Réale et al. 2010). All of these components together

manifest in a particular movement path that can be observed from the remotely-recorded locations of a collared animal.

We studied the movement behavior of moose (*Alces alces*) in northeastern Minnesota to determine if behavioral syndromes can be detected in this population. During the last decade, the moose population in northeastern Minnesota declined in excess of 50%, with climate change suspected to affect many known drivers of moose mortality (Lenarz 2012). This dramatic decline is a serious conservation concern because of the species' integral role in the boreal ecosystem and its economic and cultural importance. As a keystone species, moose sculpt the local plantscape through browsing and redistribution of nutrients (Bump et al. 2009). Moreover, as prey items of the gray wolf (*Canis lupus*, a keystone predator), this species is deeply woven into the web of boreal life. The population resides at the southern limit of the boreal forest in an area subject to land-use and land-cover modifications (e.g., timber harvest, mineral extraction, blowdown events, forest fires) and climate change (an expected change of $> 6°$ C over this century; IPCC 2007); it is imperative that management plans address as much of the population as possible. An improved understanding the animals' behavioral patterns may help better understand the decline and inform management plans so that they are more likely to yield success.

The goal of this project was to use location data to describe the extent to which moose in northeastern Minnesota vary in their behavior, and whether behavioral patterns are driven more by the landscape or by individuality. This example is intended to contribute to the greater question: can we detect behavioral syndromes in wildlife from remotely-collected location data? The ultimate purpose is to assess whether the range of behavioral variation in a population might imply a need for diverse management strategies, and to encourage more applied research on behavioral syndromes.

Study Area

The Grand Portage Indian Reservation encompasses 192 km^2 of extreme northeastern Minnesota, bordered by Ontario, Canada on the north and Lake Superior on the east. An estimated 30-80 moose reside at least partially within the reservation

boundaries, and since 2010 the Grand Portage Department of Biology and Environment has attempted to maintain 30-35 collared individuals each year. This area is also occupied by other large wildlife species: white-tailed deer (*Odocoileus virginianus*), gray wolves (*Canis lupus*), and black bears (*Ursus americanus*).

Grand Portage is densely forested with deciduous, coniferous, and mixed forest stands. Common tree species include white spruce (*Picea glauca*), black spruce (*Picea mariana*), jack pine (*Pinus banksiana*), balsam fir (*Abies balsamea*), white birch (*Betula papyrifera*), and trembling aspen (*Populus tremuloides*; Street et al. 2016). Sources of forest disturbance include timber harvest and forest fire. The terrain is topographically rugged, with relatively high and steep ridges and bluffs exceeding elevations of 500 meters. The forested hills are dotted with ponds, wetlands, bogs and other water features.

Methods

Overview

Location data (i.e., spatial coordinates of where an individual was located at a particular time) were collected for 35 moose. The Universal Transverse Mercator (UTM) coordinates and associated dates and times were used to calculate movement-based behavioral metrics at a path-level scale and at a greater home range scale. Maps of land-cover and terrain metrics were used to quantify features of the environment. Behavioral metrics were used in a cluster analysis to look for patterns within and among individuals in the population. Environmental variables were used to determine which differences were attributable to landscape features; unexplained differences were attributed to either individuality in animals or unmeasured variables. Analyses utilized R version 3.4.1 (R Core Team, 2017), and ArcMap (Environmental Systems Research Institute 2016).

Data Collection

Moose were captured and collared during a week-long period in January, February, or March from 2010-2015. Thirty-five individuals (28 females and seven males) were collared and tracked for one to five winters and zero to three summers.

Moose were captured by aerial darting and immobilized with either a combination of carfentanil and xylazine or thifentanil and xylazine. Naltrexone and tolazoline were used as reversal agents, and all captures were conducted in accordance with the American Society of Mammalogists wild animal care guidelines (Sikes et al. 2011). Animals were outfitted with GPS (global positioning system) collars (Sirtrack Ltd., Havelock North, Hawkes Bay, New Zealand and/or VECTRONIC Aerospace GmbH, Berlin, Germany) that recorded individual locations at intervals of 15, 20, 30, 60, or 120 minutes, depending on the season and technical capacity.

Data Cleaning

Location data were cleared of unnatural or abnormal fixes attributed to (1) animal capture events, (2) mortalities, (3) collar transfers between individuals, and (4) collar recording errors.

(1) Animal capture events

We recorded the final day, T_f, of capture events for each year. Typically, one multi-day capture event occurs toward the end of winter each year. We also recorded each year that any given individual was captured or recaptured. For a year in which an individual was captured, we removed all locations from that year leading up to T_f, all locations on T_f, and all locations through the next two days (T_{f+2}). Thus, locations for a new collar year were not included in analysis until three days after the last capture event of the season.

(2) Mortality

Dates of mortality were recorded for each deceased individual when a mortality signal was sent by a radio collar. We removed all locations recorded on the day of a mortality, as well as all successive locations for the rest of that year (until the collar was re-deployed, when applicable). Locations recorded during the last few days leading up to mortality were inspected for any indications of earlier mortality.

(3) Collar transfers

Often, a collar that was removed from one individual was re-deployed onto a different individual the following year. We confirmed the proper transfer of fixes from each collar ID number to its new animal ID number whenever collars were re-deployed.

When necessary, fixes were transferred to the correct individual and were then trimmed according to the capture protocol, (1), above.

(4) Collar error

Locations were screened to remove unnatural movements caused by spurious collar recordings. A movement rate threshold was set at 30 km/hr, above which steps would be considered biologically impossible (van Beest et al. 2013). After standardizing steps to 2-hour intervals, the maximum average movement rate was 8.4 km/hr.

Calculation of Movement-Based Behavioral Metrics

Home ranges

Utilization distributions were calculated for each individual for each season-year that included at least 300 recorded locations. We used the 95% isopleth of the utilization distribution calculated with biased random bridges (BRBs), a movement-based kernel method available in the R package "adehabitatHR" (Benhamou 2011, Calenge 2006), to approximate the seasonal "home ranges" of each animal. Like the Brownian bridge method, the BRB method makes use of autocorrelation in location data by incorporating the time intervals between pairs of successive locations. However, while the Brownian bridge method assumes all diffusive movement between locations, BRBs consider more biologically realistic advective-diffusive movement, applying drift toward the next location (Benhamou 2011). BRBs also offer distinction between active and resting periods. Although we were unable to include activity information due to both the natural history of our system and technical limitations (see parameterization of L_{min} in **Box 1**), the advective-diffusive BRB method still offered the most practical and biologically-relevant home range estimates when compared to purely diffusive-movement-based or simply location-based methods (Benhamou 2011).

Site fidelity and space-use sharing

Site fidelity was assessed as the volume of intersection (i.e., kernel overlap) between an individual's home ranges from one year to the next. Summer and winter home range fidelity were assessed independently. In most cases, site fidelity was

calculated for the home ranges of subsequent years (e.g., overlap between winter 2010 and winter 2009). In two cases, a year of data was missing between seasons, so the home range was compared with the one two years prior. Many individuals did not have enough data to calculate site fidelity, which resulted in missing values. Ultimately, the site fidelity behavioral metric was omitted from the final analysis.

Space-use sharing was calculated similarly using the volume of intersection between home ranges of each individual with other collared individuals during a given season and year. Therefore, the calculations only describe how much an individual's home range was shared with other collared individuals. It was not possible to assess space-use sharing with un-collared individuals. The metric was reported as an individual's mean kernel overlap with all other collared individuals for that season-year.

Step metrics: velocity, daily path length, and net daily displacement

A "step" refers to two successive locations and the time and space between them. Locations were recorded at intervals of 15, 20, 30, 60, or 120 minutes; for all *step metrics*, paths (i.e., individuals' series of steps) were re-discretized to the coarsest temporal resolution of 120 minutes so that results would be comparable among individuals. The process of re-discretization included setting a reference date and time as a starting point, adding missing values at multiples of the theoretical time interval, rounding the timing of coordinates, and interpolating to fill in values where locations were missing.

Velocity was measured by dividing the straight line distance between each pair of successive locations by their temporal separation (i.e., 120 minutes). It was reported as an average for an individual during a given season-year.

Daily path length is the sum of the lengths of all steps taken during a day (24 hours). This metric was calculated from the re-discretized paths for each day and then averaged for each individual and season-year.

In contrast, net daily displacement is the straight-line distance between the first and last locations recorded during a day. This value also was calculated from the re-discretized paths for each day and then averaged for each individual and season-year. It

may reflect whether an animal was leaving and returning to a common area or engaging in more exploratory behavior.

Step metrics: turning angles

A turning angle is the measured change in direction between two adjacent steps. As angular data, turning angles can be summarized by circular means and concentrations. Angles were extracted from path or trajectory information using adehabitatHR. Empirical data were plotted on rose diagrams (circular histograms) for each individual, separately for different season-years. A mean and a concentration (kappa) were fit to each set of data using the R package "CircStats" (Lund and Agostinelli 2012). These values were used to simulate a new dataset, which was compared to the empirical one to assess the accuracy of the calculated means and concentrations in representing empirical patterns.

A few problems were common in comparing the empirical and simulated diagrams. Some diagrams that appeared to be comparatively uniform had high concentration values. Also, at times it appeared that the data were mainly concentrated around two means (near 0 and 180 degrees). To address this, each dataset was given a subjective turning activity score. Scores were designated according to the guidelines specified in **Box 2**.

A binary second designation, kappa direction, was determined based on whether the individual's turning behavior was more concentrated in the forward direction or the backward direction (i.e., was kappa greater for angles between -0.5π, 0, and 0.5π, or between $\pm 0.5\pi$ and $\pm\pi$?). When the direction of travel was more concentrated in the forward direction of travel, the individual was assigned a value of 1. When the direction of travel was more concentrated in the reverse direction, the individual was assigned a value of 0.

Land cover type use

Individual use of different landscapes was quantified by finding the difference between available and used cover types. Land cover types were extracted from the 2013 northern Minnesota landcover map offered by the Remote Sensing and Geospatial Analysis Laboratory at the University of Minnesota, with level 2 cover designations at a

resolution of 15m pixels. The raster was funded by the Minnesota Environmental and Natural Resources Trust Fund and combined multitemporal Landsat 8 imagery and aerial light detection and ranging (LiDAR) with object-based image analysis.

To quantify an individual's use of the various cover types, the 95% utilization distribution kernels calculated from all location data for home ranges were overlaid on the landcover raster. The density at each point within the home range was extracted with the associated cover type value and then densities were summed, aggregating by cover type. Proportions of use were calculated from the sums.

Several individuals had locations in Canada, which is outside the extent of the landcover map. Proportions of use for these animals were normalized by dividing the summed densities by the total volume of the kernel that was within the coverage area.

Proportions of availability were calculated from a circular buffer with a radius of 2 km at the centroid of the home range. The length of the radius was selected based on the value needed to produce a circle with an area equivalent to the areas of the largest home ranges of all individuals during summer or winter.

Terrain ruggedness (used)

Grand Portage is more topographically diverse than the majority of northern Minnesota. The study area includes several sheer cliffs, which can affect wildlife movement patterns. Topographical variability was calculated as a behavioral metric as well as an environmental factor (see: "Terrain ruggedness (general)"). A Slope and Aspect Ruggedness Index (SARI) was calculated (Bragin et al. 2013; Nelleman and Fry 1995):

$$SARI = \frac{(standard\ deviation\ of\ slope) * (variety\ of\ aspect)}{(standard\ deviation\ of\ slope) + (variety\ of\ aspect)}$$

Slope and aspect data were extracted from the LANDFIRE database (LANDFIRE 2010). A SARI layer for the study area was created in ArcMap by using the focal statistics tool and creating a 3x3 cell neighborhood with standard deviation as an operator on the slope layer and variety as an operator on the aspect layer.

Average SARI was calculated within the 95% isopleth of each animal's utilization distribution and also within the circular buffer around the home range centroid. The

metric was reported as the difference between the two averages, i.e., a positive value indicated that the individual was using more rugged terrain than what was generally available in the area and a negative value indicated that an individual used less rugged terrain than what was generally available. SARI was ultimately excluded as a movement metric in the synthetic analysis and was included as an environmental variable (see below).

External and Environmental Variables

Designation of seasons

Seasons were defined functionally for this specific population and its geographic location. As such, seasons vary in length. Winter (December 1 - March 31) was defined based on the normal period characterized by snow cover and cold temperatures in this region. Summer (June 15 - September 15) was defined to encompass the period following all calving and preceding all rutting behaviors (Severud et al. 2015). Both of these seasonal behaviors (calving and rutting) can cause atypical and unpredictable movement behaviors. They were excluded in favor of the summer and winter seasons, which are nutritionally important to moose.

Climate data

Climate data were obtained from Climate Data Online via the National Climatic Data Center (www.ncdc.noaa.gov). Maximum daily temperatures and snow depth were obtained from Grand Portage (station no. 213296), but historical wind data were not available. Average daily wind speed was obtained from nearby Grand Marais (station no. 94992), approximately 55 km southwest of Grand Portage.

Seasonal severity indices

Seasonal severity indices were developed to quantify inter-annual variability. Summer and winter severity indices were created based on the known heat stress temperature thresholds of moose. Summer severity was based on maximum daily temperature, accounting for average daily wind speed (moose can tolerate higher temperatures on windier days; McCann et al. 2013). Severity points were accrued for

each day of a summer that reached 17 °C (62.6 °F) under calm conditions (defined by aviation convention as 3-5 knots, or approximately 5 mph or less) or reached 24 °C (75.2 °F) under windy (> 5mph) conditions (McCann et al. 2013).

Severity points were accrued for each day of a winter that reached -2 °C (28.4 °F; Renecker & Hudson 1986) and for each day that had a minimum snow depth of 60 cm (23.6 inches), which inhibits movement and makes locomotion more energetically expensive (Telfer 1970). Under these criteria, a single day could earn two severity points for that winter season. When data such as snow depth were unavailable, those days were omitted from the severity assessment.

After severity values were calculated for each season-year (e.g., Summer 2010, Winter 2010, etc.), values were normalized (0-1) by season. This adjustment accounted for the different indices and ranges of values for summer and winter, thereby enabling summer-winter comparisons.

Terrain ruggedness (general)

Terrain ruggedness was calculated as described above ("Terrain ruggedness (used)") for the circular buffer with a 2 km radius over the centroid of a home range. The value was reported as average SARI within the buffer.

Mortality status

A mortality status was assigned to each individual for each season-year for which there was movement data. If the individual was tracked during the next season or otherwise confirmed to be active, they were designated as alive. If the individual died during that season-year or before the start of the following season-year, it was designated as a mortality. For example, an individual who was tracked throughout winter 2010 but was confirmed dead in spring 2011 was designated as a mortality for winter 2010. Individuals who had collar malfunctions (e.g., battery failures, collars removed, collars lost during fights) were designated unknown. Most adult moose perish from health-related issues, such as brainworm, which can affect their movement patterns (Carstensen et al 2015). Thus, assigning a mortality status provided a way to recognize the individuals whose movement metrics may have been influenced by health conditions.

Habitat patch statistics

Habitat fragmentation has potential to be both beneficial and detrimental to moose; depending on the type of the disturbance, fragmentation could serve as a corridor or a barrier (Bartzke et al. 2015). The cover types that were identified to be most important to moose in this study (based on the difference between use and availability) were deciduous and coniferous forest. Three fragmentation statistics were calculated for each of the two most important cover types (deciduous and coniferous forest) within circular buffers, using the R package "SDMtools" (VanDerWal et al. 2014). Mean patch area gives the mean patch area for that cover type within the defined area. Edge density gives the length of patch edges per unit area. Patch cohesion "measures the physical connectedness" of the patches of that cover type within the defined area (VanDerWal et al. 2014).

Synthesis

K-means clustering

Behavioral metrics were analyzed using k-means cluster analysis to identify whether behavioral patterns were distributed among somewhat-distinct groups or more continuously. K-means cluster analysis is available in the base package "stats" in R, and was calculated by the default algorithm defined in Hartigan and Wong (1979). Summer data and winter data were assessed separately, due to very different ranges of values between the two seasons.

The number of clusters must be pre-specified to run the analysis, and it is important to not guess or assume the number of clusters but to rather let the data determine how many clusters there should be. There are at least two options for determining an appropriate number of clusters. The option utilized for this project was to define the number of clusters ranging from one all the way through ten, saving the R^2 value from each analysis. Then, R^2 was plotted against the number of clusters and an asymptote was identified that was used to determine which number of clusters was the most reasonable. A more extensive option would be to complete the aforementioned steps and then calculate gap statistics by using principal components to create reference data

(Tibshirani et al. 2001). The results of k-means clustering are sensitive to input values, and data must be prepared before performing the analysis (**Box 3**).

Nonmetric Multidimensional Scaling (NMDS)

Observations were also related by non-metric multidimensional scaling (NMDS) using the R package "vegan" (Oksanen et al. 2017). Data were reduced to two dimensions using Canberra distance as the dissimilarity index to sort individuals based on the closeness of their relationships. Observations (i.e., the set of calculated metrics for an individual during a given season and year) were plotted by coordinates representing their values on the first two NMDS axes (dimensions).

Two different categories of plots were made. First, NMDS distances and coordinates were calculated based on the variables that were used to define the k-means clustering. Observations were then plotted and colored by cluster ID and other non-numeric or discrete variables to look for patterns in grouping and variability.

In the second category of plots, NMDS distances and coordinates for observations were calculated based on environmental variables. The observations were plotted and colored by cluster ID to look for any patterns that might be apparent due to similarities and differences in environmental conditions (i.e., did individuals that experienced similar environmental conditions tend to be grouped in the same behavioral clusters).

Miscellaneous variable relationships

Analysis of variance (aov) was used to model values of behavioral metric variables by cluster group. Variables were untransformed, with outliers omitted. Linear mixed effects models were used to test for relationships between and among behavioral and environmental variables (R package "lmerTest"; Kuznetsova et al. 2017). Details about specific models are listed in **Appendix 2**.

Results

Variable transformations: distributions and outliers

Most of the measured behavioral variables had normal distributions of values. In many cases there was a notable amount of variability, including ranges of values that may be considered broad in their biological interpretation. **Figure 1** illustrates the distributions of values for a selection of behavioral metrics that are relevant to moose management.

Of the 40 different metrics calculated for the two seasons, six had distributions that were skewed enough to require transformation prior to normalization: net daily displacement, diffusion coefficient, home range area, and average space-use sharing in winter, plus coniferous forest selection in both summer and winter. Over half of all metrics had outliers (values above or below 1.5 times the interquartile range), which were omitted. The metrics with more than five outliers were either omitted from analysis completely or converted to binary values. For example, **Figure** shows the distribution of the metric "space-use sharing" for winter seasons. There were 32 observations with values < 0.05 and the remaining 32 observations ranged from 0.05 to 0.9; this metric was transformed from continuous numeric to binary, in which values of < 0.05 were assigned as 0 and values > 0.05 were designated as 1. A full table of variable transformation results is listed in **Appendix 1**.

Cluster analysis

K-means cluster analysis was first applied to the winter season data, which had larger sample sizes than summer. Omitting observations with missing values (which are not dealt with in k-means) reduced the winter sample size from 68 individual-season-years to 48. After entering all 13 of the transformed selected variables, it was unclear how many clusters should be used because there was no clear asymptote in a graph of R^2 vs. number of clusters. However, this approach would require designating 13 clusters to explain at least 80% of the variation between observations; such a result is non-informative.

The next approach omitted variables that were subjectively determined to be the least likely to be informative, leaving five variables for inclusion (daily path length, net

daily displacement, turning direction, diffusion coefficient, and home range area). With these variables, a high R^2 of 0.95 was achieved by defining four clusters ($R^2 = 0.63$ when reduced to three clusters). However, further analysis revealed that all of the differences between the groups were based on their values for the two binary metrics, turning direction and diffusion coefficient. The algorithm defined the four clusters based on those two values (0-0, 0-1, 1-0, or 1-1), which accounted for differences between groups but not in a meaningful way.

The third approach omitted all binary variables and used optimization to find the combination of metrics (combining as few as two or as many as seven metrics) that would yield the highest R^2 value while preferring to define fewer clusters. Continuing to add metrics beyond seven did not increase scores. The optimal approach included only two metrics, daily path length and net daily displacement. Defining five clusters based on path length and displacement allowed for a sample size of 62 and yielded an R^2 of 0.94 (with four clusters $R^2 = 0.90$, three clusters $R^2 = 0.85$, and two clusters $R^2 = 0.71$).

Distances between observations were calculated using NMDS with two axes based on the two variables used in clustering, and their coordinates were plotted and colored by cluster ID (**Figure 3**). Despite this approach yielding the best results in the k-means analysis, there was no distinct separation among the cluster groups, other than an apparent change in variance.

The five cluster groups differed significantly in their average values for the two variables that were used to define them (i.e., daily path length and net daily displacement). Values of these variables spanned a wide range of values; average daily path length ranged from 289 meters for individuals in cluster one to 1325 meters for individuals in cluster five (**Figure 4A**). Average net daily displacement for groups ranged from 115 meters (cluster one) to 720 meters (cluster five; **Figure 4B**).

Analysis of variance among the five clusters identified that, in addition to daily path length and net daily displacement, clusters differed significantly in diffusion coefficient ($F = 9.1$, $p << 0.001$) and home range area ($F = 18.9$, $p << 0.001$). Daily path length, net daily displacement, and home range area were all highly correlated (all Pearson's coefficients > 0.70), while diffusion coefficient was not (all Pearson's

coefficients < 0.60). Resulting patterns were the same when two clusters were defined instead of five.

To look for possible relationships between cluster ID and the non-numeric and binary variables, observations were plotted by their NMDS coordinates and colored by their values for these variables. There were no visible patterns on plots marked by diffusion coefficient, turning direction, or space-use sharing, suggesting that differences in values for the clustering variables (daily path length and net daily displacement) were not related to values for these binary behavioral variables (**Figure 5A-C**). Additionally, there were no visible patterns on the plots by sex and mortality status, suggesting that the behavioral differences characterizing the cluster groups were not attributable to these variables (**Figure 5D** and **5E**).

Observations were also plotted on NMDS axes that were calculated from all quantitative environmental variables, and then colored by cluster ID (**Figure 6**). Like-colored observations did not group together on the plot, suggesting that differences between clusters were not due to exposure to similar environmental or external conditions. While **Figure 6** shows the observations plotted on environmental axes NMDS1 and NMDS2, observations were plotted on all possible combinations of environmental axes one through five (NMDS1, NMDS2, NMDS3, NMDS4, and NMDS5) to check for patterns in the arrangement of observations. No patterns were observed on any combination of axes.

For individuals that had more than one winter of observations, these observations were plotted separately by individual on the environmental NMDS axes one and two (**Figure 7**). The relatively close positioning of points on these plots shows that observations tended to be more similar to each other than random. The patterning suggests that individuals tended to be exposed to similar environmental conditions from year to year.

This clustering method did not yield high rates of reclassification, regardless of how many clusters were defined. Of 22 individual animals that had more than one winter of data, only seven (32%) were reclassified to the same cluster at least once when defining five clusters. When reducing to two clusters, the reclassification rate was only 59% (13 of 22 individuals).

Due to the small sample size, a full separate analysis was not done for summer; when observations with missing values were omitted, the number of observations decreased from 33 to 22.

Behavioral metrics

Relationships between the behavioral metrics and environmental measures were assessed using mixed effects models. A full table of these models and their results is listed in **Appendix 2**.

Velocity, daily path length, and net daily displacement

The metrics velocity, daily path length, and net daily displacement were all highly correlated; models revealed the same patterns for these three metrics. In a linear mixed model of velocity with season as the fixed effect and sex and animal ID as random effects, velocity was much slower in winter than in summer (coefficient = -33; t = -12, p < 2e-16). Similarly, daily path length and net daily displacement in winter were much less than in summer (t = -12.23, p < 2e-16; t = -9.66, p = 0.03.3e-15).

A linear mixed model of winter velocity by sex with animal ID as a random effect showed that males traveled at higher velocities than females; ten out of the 64 observations included were male (coefficient = 8.5, t = 2.4, p = 0.02). The same pattern was not noted from the summer observations, but the sample size was three males and 30 females (t = 0.023, p = 0.98). Winter daily path length and net daily displacement were greater for males than females (t = 2.097, p = 0.0399; t = 2.835, p = 0.00687).

Models of velocity, daily path length, and net daily displacement by mortality status and season with sex and animal ID as random effects suggested that all three values were smaller for individuals that ended up dying before the start of the following season when compared to individuals that were known to be alive the next season (t = -2.811, p = 0.00601; t = -2.408, p = 0.018; t = -2.073, p = 0.041). The sample sizes were 11 and 83 for individuals that died and were recorded alive, respectively.

Diffusion coefficient

According to the mixed model of diffusion coefficients with season fixed and sex and animal ID random, diffusion coefficients were significantly smaller in winter than in summer (coefficient = -0.636, t = -4.568, p = 2.06e-5). No other significant differences were noted.

Home range area

With home range area modeled by season (fixed) with sex and animal ID random, home range areas were much smaller in winter than in summer (coefficient = -2. 653, t = -5.948, p = 9.51e-8). Home ranges were also smaller for individuals that died before the next season, i.e., with mortality status fixed and sex and animal ID random (coefficient = -1.771, t = -2.109, p = 0.0376).

Turning angles

The angle scores that were assigned based on visual inspection of the distributions of values were non-informative. Kappa directions showed that 82% of individuals (n = 80 of 97) had turning angles primarily in a forward direction, while 18% of individuals more consistently turned back toward directions that they had come from.

Site fidelity

For summer seasons, measures of site fidelity were available for only five individuals. Two of these five had two measures of site fidelity (i.e., three summers of data were available). Values ranged from 0.12 to 0.51, with a mean of 0.29 indicating that individuals returned to some of the same space that they had used the previous year, but the majority of their space use was in new areas. The distribution of values appeared to be normal, although of a very small sample size.

Twenty two individuals had measures of site fidelity for winter seasons, with five of the 22 having two or more values (up to four). Values ranged from 0 to 0.55, with a mean of 0.09. Values were highly right-skewed, with seven of the values being zero and only nine of all values being greater than 0.1. There were no consistent patterns within individuals with more than one value; two individuals had values that were very close and a few had a very wide range of values.

Use of forests, water, and fields

Use of land cover types was assessed at a broad scale and a specific scale. For broad-scale analysis, land cover types were grouped into forest, aquatic, and field. The volume of the utilization distribution over each cover type was extracted, omitting individuals that had more than 50% of their kernel over Canada (where the land cover map was unavailable).

Proportions of use of forest types (conifer, deciduous, mixed, and regenerated forest) ranged from 0.48 to 1, with a mean of 0.85; summer and winter means were not significantly different ($t = -1.62$, $p = 0.1116$). Distributions of values for both seasons were heavily left-skewed, with more values closer to 1 than to 0.5.

Use of aquatic cover types was slightly different by season. In a linear mixed model of proportion of aquatic use by season with sex and animal ID as random effects, the proportion of the utilization distribution over aquatic cover types was slightly but significantly less in winter than in summer (coefficient = -0.038, $t = -3.381$, $p = 0.00136$). Aquatic cover types include open water, emergent wetlands, and forested wetlands. Ranges of values were similar (0-0.22), but the distribution of winter values had a much heavier right-skew than summer.

Field cover types (grassland, hay and pasture, row crops) were generally not highly utilized. Values ranged from 0 to 0.11 and the mean of 0.025 was not significantly different by season ($t = 0.76$, $p = 0.45$). Values were very heavily skewed right, with most animals having minimal use of these cover types but a few animals used them heavily. Patterns of utilization of developed space was similar; values ranged from 0 to 0.025, with a heavy right skew. This assessment does not account for the differences in availability of these cover types, which are explained in the next section.

Differences between use and availability of land cover types

A variant of resource selection was calculated by finding the difference between the proportion in which a cover type was used and the proportion in which it was generally available within the local area. Negative values indicate that the cover type was used in a proportion less than in which it was available, and positive values indicate that it was used more than its general availability on the landscape.

The only difference in use that varied between seasons was that of forested wetlands. The mean difference in winter was -0.036 and in summer it was -0.010 ($t = 2.26$, $p = 0.0295$). In winter almost all values were negative but ranged from -0.13 to 0.037. In summer the values were much more concentrated around zero. Open water was used less than its availability in every winter observation, although most values were very close to zero. There was a larger spread of values during summer, ranging from -0.1 to 0.06.

In both summer and winter, use of coniferous forest was about half positive and half negative among individuals. For both seasons, most values were slightly below zero but there was also a large set of values ranging upward to 0.5 and a smaller set ranging down to -0.22. Use of deciduous stands was evenly positive and negative in winter, but more than half of values in summer were positive. Mixed forest was less common than other forest types, but the majority of its use was positive, with a wide range for both seasons and a mean of 0.05.

Differences in use and availability of developed land were small in magnitude but mostly negative. The mean was -0.014 and was not different between summer and winter. Similarly, values for emergent wetlands were mostly negative and all very small in magnitude, averaging -0.0035. The remaining cover types, regenerated forest, grassland, hay and pasture, and row crops, were minimal in occurrence on the landscape, and their use-availability differences were almost all very close to zero.

Discussion

Explanation of Results

The k-means cluster analysis of selected metrics for this dataset did not reveal evidence for distinct behavioral types based on movement in this population. It is not unlikely that behavioral types exist, given the literature available on other closely-related species (e.g., Found and St. Clair 2016; Bonnot et al. 2015). Therefore, it remains important to determine the distributions of behaviors that are related to cover types and other habitat features that we try to manage for wildlife populations.

After several approaches to k-means cluster analysis, it remained unclear how to determine which variables were informative (i.e., which should and should not be included). Although binary variables are regarded as acceptable for inclusion in k-means cluster analysis, including multiple binary variables overwhelmed the other metrics and the groupings were based almost exclusively on those binary variables. After omitting binary variables, cluster groups were best defined by highly correlated variables even after their weights were adjusted to account for their correlation. Visualization of the clusters showed some separation, but nothing clear enough to suggest distinct groups. It

is inconclusive whether or not these variables were informative of behavioral individuality. However, the utilized metrics are straightforward to calculate from location data, so if further studies can confirm their utility then use of these metrics would allow straightforward inter-study comparisons.

The seasonal differences that were calculated between movement metric values are consistent with what is already known about moose behavior. Specifically, the movement of this species generally decreases in winter (Peterson 1955), which results in smaller observed winter home ranges in some, but not all, populations (Hundertmark 2007). In our study, this seasonal change is reflected in home range sizes, velocity of travel, distance traveled per day, and net daily displacement. Although the results are not novel, they demonstrate that the approach that was used in this study was at least sufficient for detecting large-scale differences in movement behavior. Further, when analyzing general use of broadly-classified land cover types, results were consistent with what is known about the Minnesota moose population: forested areas are primary habitat (Peek et al. 1976), and aquatic features are more important in summer than in winter (Peek 2007).

The other noteworthy results from the mixed-effects models were differences in movement behavior with mortality status. Generally, individuals moved less and more slowly if they died the following season, compared to the individuals that were reported alive the following season. Most mortalities of moose in Minnesota are caused by health issues, which do manifest in behavioral changes (Carstensen et al. 2015). It would be beneficial for wildlife managers to be able to detect health declines from changes in movement behavior, but the methodology would need to be repeated on a dataset with larger sample sizes. Further, for the results to be helpful, there would need to be minimal overlap between the ranges of values for putative sick and healthy individuals.

Should we manage for the average?

To what percentage of the population does a management plan designed for the average moose actually apply? Wildlife management plans are based on behaviors that can vary with context and are therefore more difficult to quantify than body dimensions; assessment requires more complicated methods of multivariate analysis. From the remotely-collected data, we observed that there is a biologically-meaningful amount of

variability in behavior among animals. For example, during the summer of 2014, individuals' home range areas ranged from 1.5 km^2 to 13 km^2, which demonstrates a great difference in space use. Using cluster analysis and non-metric multidimensional scaling plots of behavioral data, we saw no strong separation into distinct groups. Further, the variation was not explained by the measured environmental variables. Therefore, there might not be a need to manage for different groups in this population, but there could be a need to manage for a wide range of behaviors, including many individuals that deviate far from the average.

The management considerations most relevant to the Minnesota moose population are harvest, predation, disease and parasites, and the availability of suitable habitat (MNDNR 2011). Moose harvest was suspended indefinitely in 2013, although it has been suggested that as long as the bull:cow ratio remains above 0.67, the population-level impact of hunting is minimal (MNDNR 2011). Predation on moose by wolves accounts for about 35% of adult moose mortality in northeastern Minnesota (Carstensen et al. 2015). However, hunting wolves in Minnesota has been illegal since 2014 and therefore the wolf population is not subject to management for the benefit of moose. The third consideration, disease and parasites, accounted for 63% of recorded adult moose mortalities (Carstensen et al. 2015). Overlap in space-use between moose and whitetail deer is expected to increase the risk for disease and parasite transmission, but the Department of Natural Resources has been monitoring deer densities across the state and they are deemed to be at acceptable levels; decreasing deer is not expected to have a large impact on moose recovery (MNDNR 2011).

The fourth management consideration, habitat availability, offers more options for intervention. Habitat patches can be altered using various patterns of timber thinning and cutting, promoting and protecting certain growth types or communities, using fire to promote regeneration, protecting key cover types, etc. (MNDNR 2011). However, the chance for success in conserving and promoting suitable habitat depends on having an accurate definition of suitable habitat. If there is too much variation in behaviors, such as selection for different cover types or the amount of space required, then multiple approaches may be needed to address a greater proportion of the population. Further

research must be done to determine how different management applications will impact the movement and reproduction of individuals in the population.

Recommendations for Future Studies on Behavioral Syndromes

Quantifying the distribution of values for remotely-calculated behavioral metrics might be sufficient for answering some questions about individual variability in wildlife behavior. However, for other research questions, it might be necessary or preferable to identify particular behavioral types (of a population's behavioral syndrome) from remotely-collected data. The following considerations might be helpful for working toward that goal.

First, a retroactive approach to behavioral analysis has potential to conflict with the best practices of project design, including defining the research question and planning data analysis before gathering the data. Therefore, when using an existing dataset, it is crucial to maintain this order and select a dataset that meets the requirements of the analysis. Unfortunately, such data may not be available for many species or for populations of concern, and results from related species or geographically-distant populations might not be transferable.

Our recommended approach would be to first conduct an in-field behavioral assay on a large sample of the population that can be monitored simultaneously (i.e., assess different individuals during the same general timeframe). Meanwhile, the movement of these individuals should also be tracked at intervals that are consistent among individuals. Ideally, movement metrics should not be correlated, and should be selected with direct relevance to the system. Behavioral scores could be assessed from the field assay first, followed by calculation of movement-based metrics. Then, an analysis such as canonical variance could be used to determine if and how behavioral types are related to the movement metrics. Such an approach would offer the best chance of finding a way to identify the movement metrics or variables that could be used to identify behavioral types remotely, if such behaviors exist.

When in-field behavioral assays are not possible, it might still be possible to parse behavioral patterns from remotely-collected data. Other potential benefits of this approach include the possibility of using adequately-designed existing datasets in order to maximize what we can learn from what is available, without needing to invest large

amounts of additional funding. Without the influence of human intrusion that can be problematic in in-field assays, remotely-collected data are direct observations of natural behavior. Standardizing analytical methodologies would enable wildlife managers to apply this approach to their own systems, and would enable comparative studies. Further, even when the analysis yields a null or a negative result, such a thorough treatment of the dataset may precipitate other useful information that is helpful for understanding individuals in the population under management.

In our dataset, the distributions of values for most behavioral metrics were normal, but five out of the six metrics that did require transformation were from the winter season. This result suggests that non-normal distributions of behavior emerge in this season of nutritional limitation and restricted movement. Thus, behavioral variability might be more pronounced under extreme conditions. When assessing behavioral patterns of animals in regions with seasonally different environmental conditions, it may be important to (1) separate data by seasons, and (2) choose the best season for data collection, if not representing all seasons, based on the research question.

After the behavioral data are collected or calculated, the analysts must consider whether or not to omit outliers. If the outliers are accurately-calculated values, then omitting these data in an analysis of individuality means omitting information about the individuals that are not average. A group of outliers may be a group of interest in itself, so these values should be checked carefully for accuracy and considered in some way.

In this study, the differences between use and availability of specific land cover types were not informative. The differences were often very small in magnitude, or there was a wide range of approximately normally-distributed variation among positive (selected) and negative (avoided) values. However, moose have been demonstrated to exhibit strong patterns of resource selections by different methods in other studies (e.g., Street et al. 2016, Laurian et al. 2012). Therefore, a different method of resource selection analysis should be used.

In addition to what was utilized in this study, there are other environmental or external variables that could also be used to help explain variability in movement behavior. For example, it might be necessary to separate daytime and nighttime movements, which could be accomplished by using solar angles at the date and time of

location. Also, there are different ways to define a home range and parts of a home range, for example the core and the periphery. If biologically relevant, distinctions could be made between behaviors in different parts of the home range. For moose in particular, variables such as distances to developed areas (e.g., roads, buildings), distance to water, and a forest's age and disturbance history could also be important.

The type and time since disturbance of a forest is particularly relevant to moose, with younger post-disturbance areas providing better forage (Renecker and Schwartz 1998). High-quality disturbance data exist and are available for download, but not in a readily-usable format. In order for natural resource managers to gain access to the data, file types should be universally compatible and bugs must be fixed. Similarly, while recently-released R packages and functions offer an incredible array of analysis options for researchers, their documentation must be improved to ensure appropriate use. It is important that more thorough documentation be available so that users can understand what these functions are doing and use them properly; if it is too easy to get results, then false conclusions may be drawn from improper use. Improved documentation of algorithms, guidelines for parameter selection, etc. would enable more people to use these methods in their research. Nevertheless, current research questions might not require the most recent methods, and "statistical machismo" should be overcome for simplicity whenever possible to develop a standardized procedure that can be used by other researchers and natural resource managers (Brian McGill, unpublished).

Summary

Over the coming decades, organisms will be presented with increasingly novel environments sculpted by changes in climate and land use. Organisms facing such changes must adapt or perish. Understanding how plants and animals respond to various types and degrees of change is essential for developing effective conservation and management strategies. While the most appealing systems to theorists are those in which behavior at a broad scale, "can be understood as the collective behavior of aggregates of similar units," in reality the individual units are biologically unlikely to be homogeneous (Levin 1992). It remains important to consider behavioral syndromes in populations of managed wildlife, and whether the distribution of variation in their behavior suggests a need for diversified management strategies. It may be possible to detect behavioral

syndromes remotely, but, depending on the system, it is likely necessary to first conduct a field study to inform the remote analysis. In building from the trials described in this paper, improving documentation, offering versatile data formats, improving raster coverage at borders, and reducing complexity should yield a method for considering heterogeneity in behavior when developing or revising wildlife management plans.

Box 1. *Biased random bridge (BRB) parameterization.* Calculating home ranges using the BRB method requires prior specification of several parameter values. This section explains each of those parameters, their meaning, selected values for this project, and justification.

D: diffusion parameter

Value: unique to individual for each season-year; units in m^2/second

Justification: The diffusion parameters were calculated with a maximum likelihood function prior to the home range calculation of each individual for each season-year.

T_{max}: maximum amount of time allowed between successive locations, after which the location pair is omitted

Value: 518400 seconds (6 days)

Justification: Since the calculation of BRB should only include those time intervals that encompass serially correlated locations (Benhamou and Cornelis 2010), we based this value on a calculation of Time to Statistical Independence (TTSI, time at which there ceases to be autocorrelation in successive observations; Swihart and Slade 1985). Non-serially-correlated pairs of locations must be omitted because there is no longer evidence that the individual was more likely to be in between those two points than anywhere else within its home range during that time frame (Benhamou 2011). We identified the individual and season-year for which the most GPS fixes were recorded (animal #9 during summer 2010, with 6673 locations) and used the R package RHR (Signer and Balkenhol 2015) to calculate TTSI on this subset of data, using the methods of Swihart and Slade (1985). For this individual and season-year, the TTSI was 542640 seconds; to be conservative, we rounded down to 518400 seconds, or six days.

An autocorrelation function of the full dataset (i.e., including all individuals and season-years) reached independence beyond nine days. In reality, there were no observations for any individual that fell within a range of five days through 13 days of separation, so at this scale this value was not critical.

L_{min}: a threshold distance between pairs of locations. The activity state of an individual with locations separated by distances less than this value may be defined as "resting"; these and can be filtered out from normal activity, which includes pairs of locations separated by distances greater than the threshold (Calenge 2006).

Value: 0.1 meter

Justification: We followed the example of Jay et al. (2012) by setting L_{min} arbitrarily low in order to avoid excluding locations based on activity level. We did not collect corresponding activity data (e.g., head movement sensor or counter) with our GPS locations, and since moose can be intensely active (e.g., browsing) without moving, we cannot use this method to differentiate between steps that are "active" and "resting" (Benhamou and Cornelis 2010).

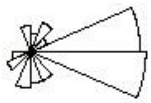
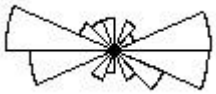
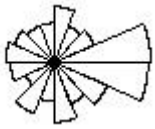
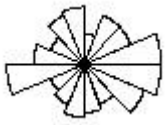
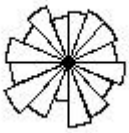
h_{min}: minimum smoothing parameter applied to all relocations (Calenge 2006)

Value: 55 meters

Justification: At the very least, h_{min} must reflect the standard deviation of the localization errors, and it should also include uncertainty of the habitat map that is being used in analysis (Benhamou and Cornelis 2010). It is recommended, although there is no standardized way to quantify, including "a random component inherent to animal behavior" (Benhamou and Cornelis 2010). Papworth et al. (2012) suggested that h_{min} should be greater than half of the mean interlocation distance. Putting this all together, we chose 55 m as the sum of the standard deviation of the least accurate collar type deployed (25 m; A. Les, unpublished data), half of the resolution of the land cover data (15 m / 2 = 7.5 m) and half of the mean interlocation distance, considering only pairs of locations that were separated by less than T_{max} seconds (45 m / 2 = 22.5 m).

Fortunately, the specific setting of this value is not of critical importance; as long as the same value is used for all individuals in the dataset, the results will be legitimately comparable at an intrastudy scale (Benhamou and Cornelis 2010).

Box 2. *Scores assigned to turning angle distributions.* The means and concentrations that were calculated to reflect patterns in distributions of turning angle values resulted in simulated data were not representative of the empirical distributions. A subjective turning activity score was assessed in order to quantify differences in directional patterns of travel.

Sample diagram	Description of distribution	Score	Explanation
	One strong mean; high concentration	1	The individual primarily travels in one direction and rarely deviates.
	Two strong means; high concentration	2	The individual has multiple preferred directions of travel and rarely deviates.
	One strong mean; low concentration	3	The individual mostly travels in one direction but commonly deviates.
	Two strong means; low concentration	4	The individual prefers multiple directions of travel but deviates.
	Mostly uniform	5	The individual does not tend to travel in a particular direction; its patterns are mostly unpredictable

Box 3. *Input factors influencing outcome of k-means cluster analysis.* The results obtained from a k-means cluster analysis are sensitive to several factors; if relevant to the dataset, these issues must be addressed.

Initial seed points

Issue: K-means clustering starts by randomly selecting a set of seed points to begin solving for the means of the clusters. Since the center of each cluster is different every time this iterative process is run, the resulting clusters might be different.

Solution: Run the analysis multiple times and compare clusters, and the cluster to which each observation (individual) is assigned (van Moorter et al. 2010).

Non-informative variables

Issue: Including non-informative variables in the analysis can obscure the underlying structure of the informative variables (Kaufman and Rousseeuw 1990).

Solution: There are some methods being developed for identifying which variables are non-informative (e.g., Lleti et al. 2004). In biological studies, when it is logical to justify a variable's inclusion based on knowledge of the study system, then that is a desirable approach (van Moorter et al. 2010).

Distribution and range of input variables

Issue: Variables that have a heavily-skewed distribution can hide meaningful structure underlying the data (Steinley 2006). Range differences between variables affect their relative contributions to the analysis (i.e., variables with a larger range of values will have a greater contribution; Kaufman and Rousseeuw 1990).

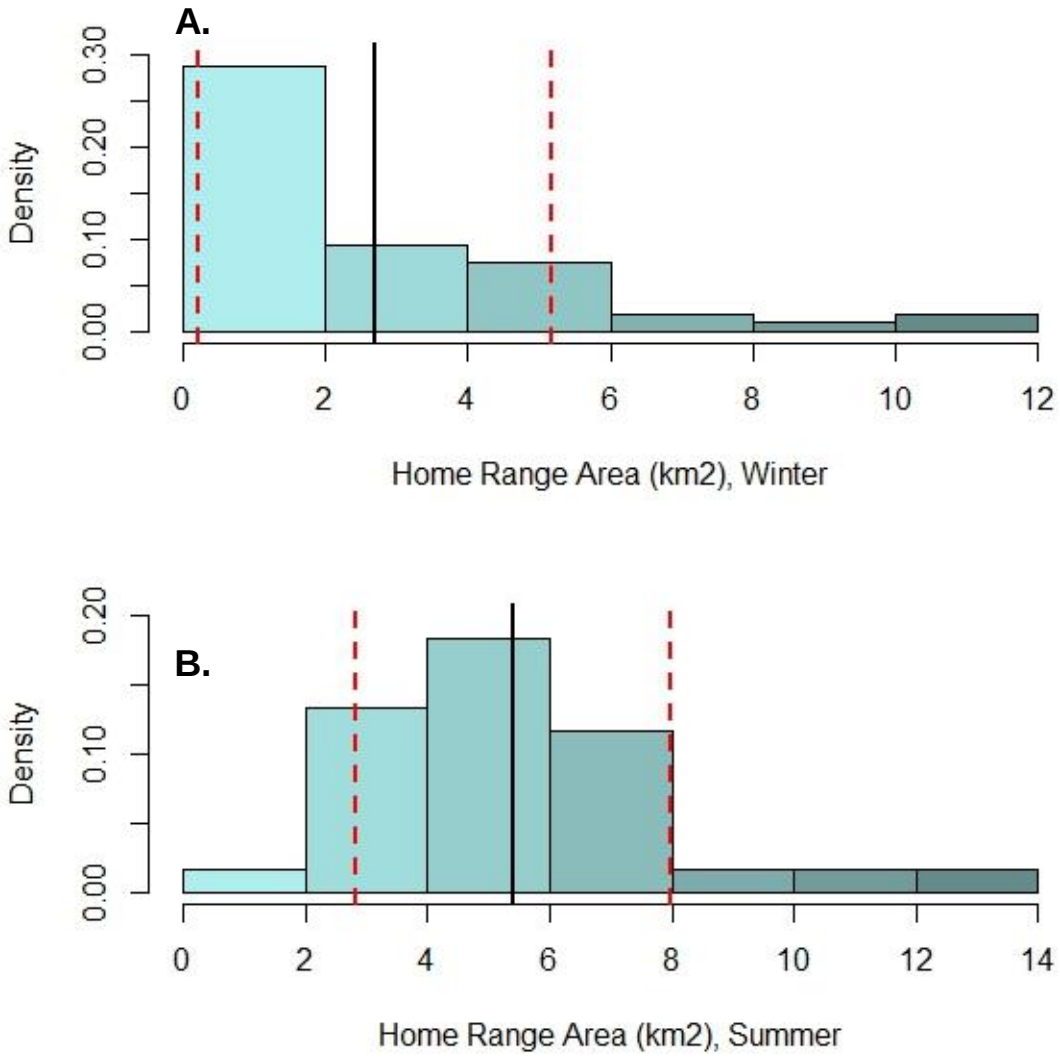
Solution: Outliers may be omitted when justified, variables with skewed distributions can be transformed, and data can be standardized to address range differences (Yingqiu et al. 2007). It may also be useful to employ differential weighting (van Moorter et al. 2010).

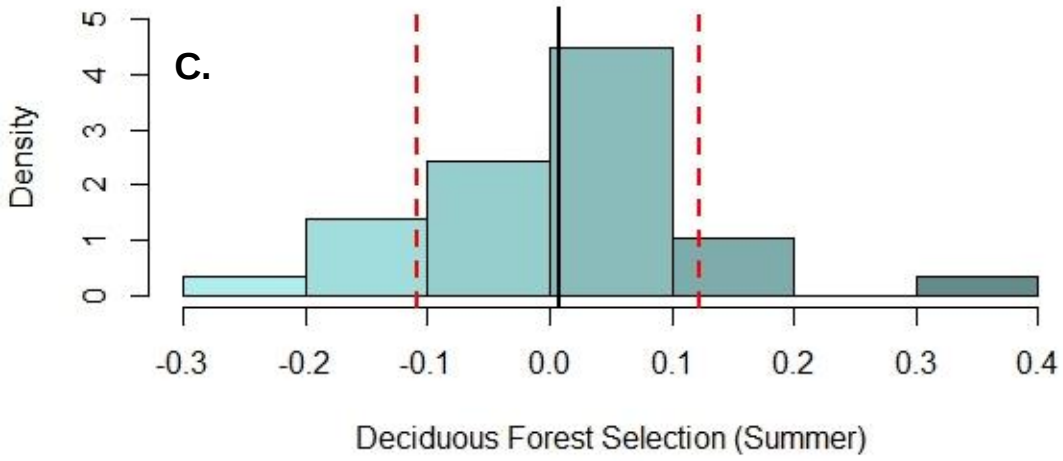
High correlation between variables

Issue: When some of the included variables are highly correlated, their influence can overcome the structural elements that are associated with other variables (van Moorter et al. 2010).

Solution: Adjust the weights of correlated values. Decrease the weight of each variable by half of their shared variance (i.e., R^2; van Moorter et al. 2010). In this project, values were only adjusted if the correlation between the variables was "large," defined as 0.5 to 1.

Figure 1. *Histograms showing means and variance of behavioral metrics relevant to moose management.* Histograms show the ranges and densities of values for home range area in winter (**A.**), home range area in summer (**B.**), selection for deciduous forest in summer (**C.**), and selection for coniferous forest in summer (**D.**). Solid vertical black lines mark the mean values and dashed vertical red lines mark the mean plus and minus the standard deviation of values. While the range of values marked by the mean plus or minus the standard deviation captures the majority observations, a notable amount of variability remains outside of those boundaries.




C.
Density
0
1
2
3
4
5
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
0.4
Deciduous Forest Selection (Summer)

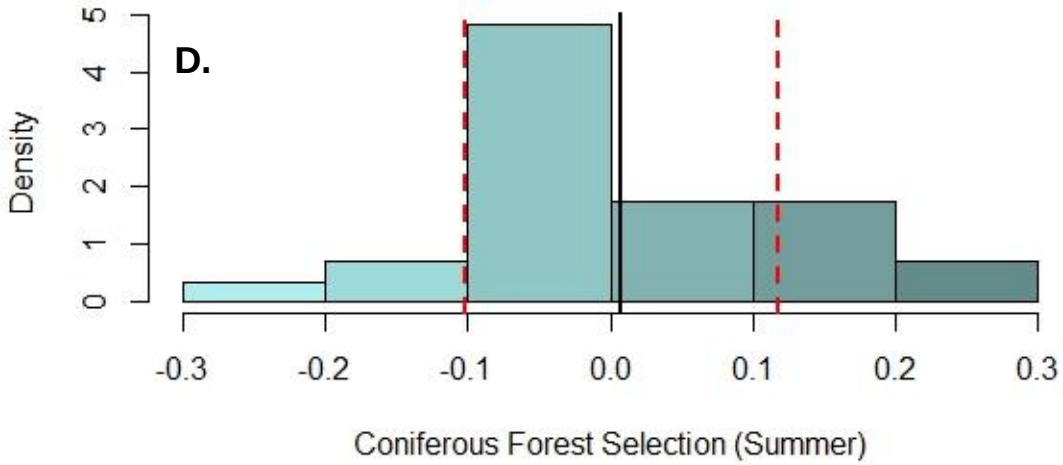

D.
Density
0
1
2
3
4
5
-0.3
-0.2
-0.1
0.0
0.1
0.2
0.3
Coniferous Forest Selection (Summer)

Figure 2. *Distribution of values for average space-use sharing during winter.* The metric, which describes how much an individual's space-use overlapped with other collared individuals, was converted to binary in which observations with values < 0.05 (n = 32) were assigned zeros and the remaining observations (0.05 to 0.9; n = 32) were assigned ones.

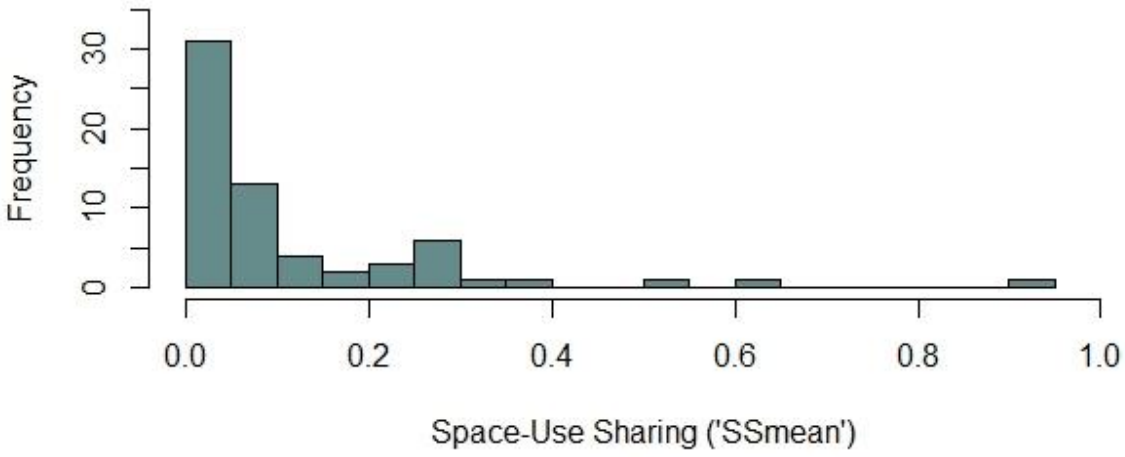
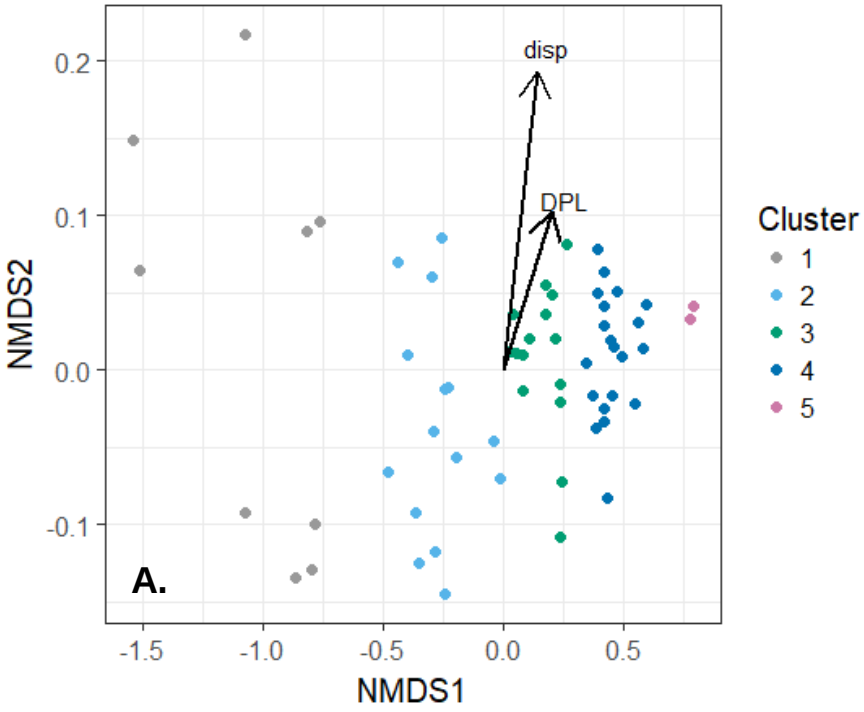


Figure 3. *Winter observations plotted by two axes of behavioral NMDS distances.* Observations are colored by cluster ID, as defined by k-means cluster analysis using the metrics daily path length (DPL) and net daily displacement (disp) to group observations into five clusters. NMDS coordinates were calculated based on similarity in the two clustering variables (DPL, disp). Outliers were omitted (**A.**, $R^2 = 0.941$, n = 62) or included (**B.**, $R^2 = 0.944$, n = 63). Including outliers added an observation to cluster number five. The overall shape of the plot changed, but the pattern remained the same; separation between clusters is not distinct in either case.



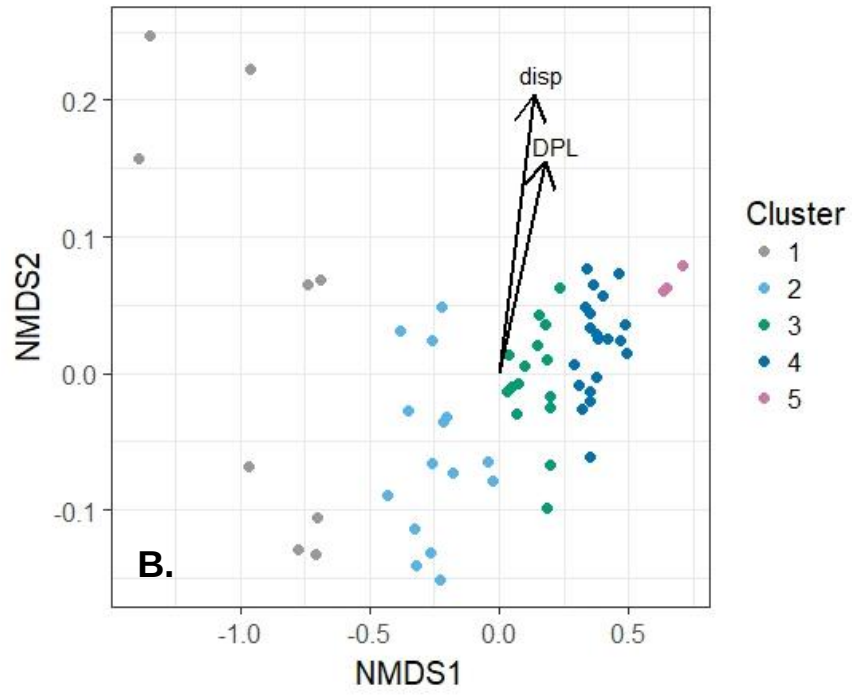


Figure 4. *Average daily path length and net daily displacement by cluster ID.* Observations of movement-related behavioral metrics were grouped into five clusters based on the closeness of their values of daily path length and net daily displacement. Average values of these variables varied significantly between clusters, and spanned a biologically-meaningful range of values. Individuals in cluster one traveled an average daily path length of 289 meters and individuals in cluster five averaged 1325 meters per day (**A.**). Average net daily displacement (i.e., distance between first and last locations within a day) ranged from 115 meters for individuals in cluster one to 720 meters for individuals in cluster five (**B.**).

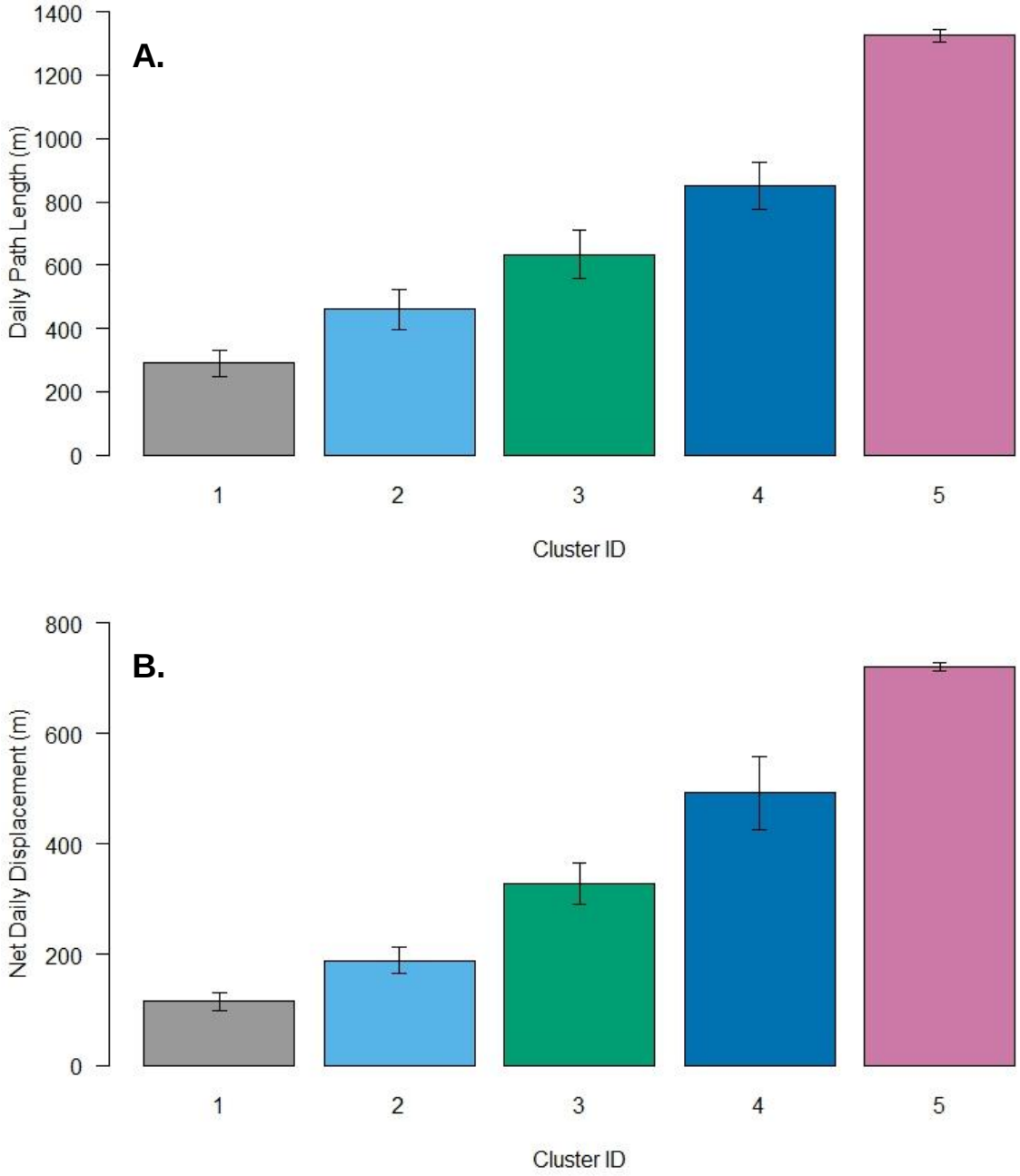
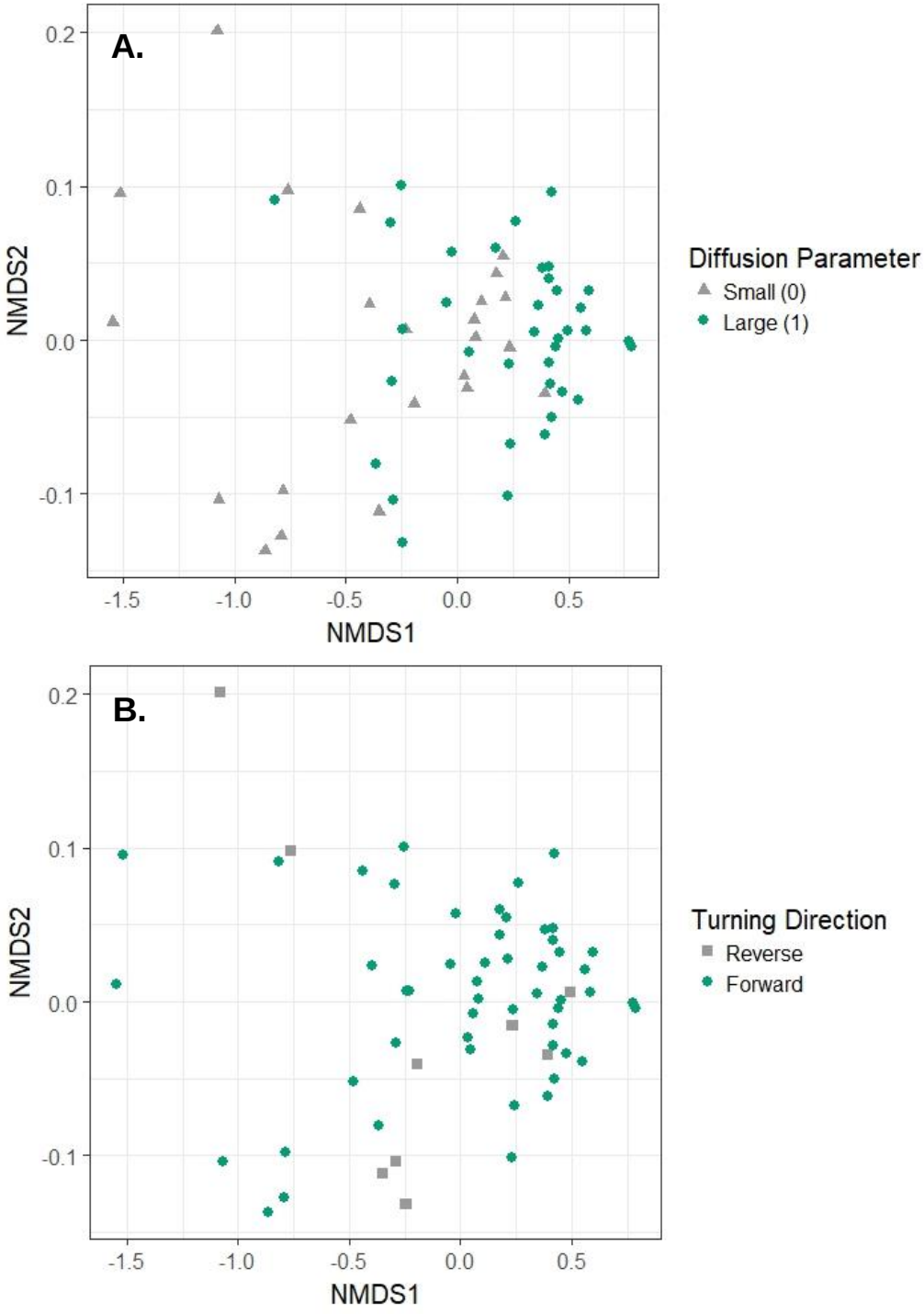
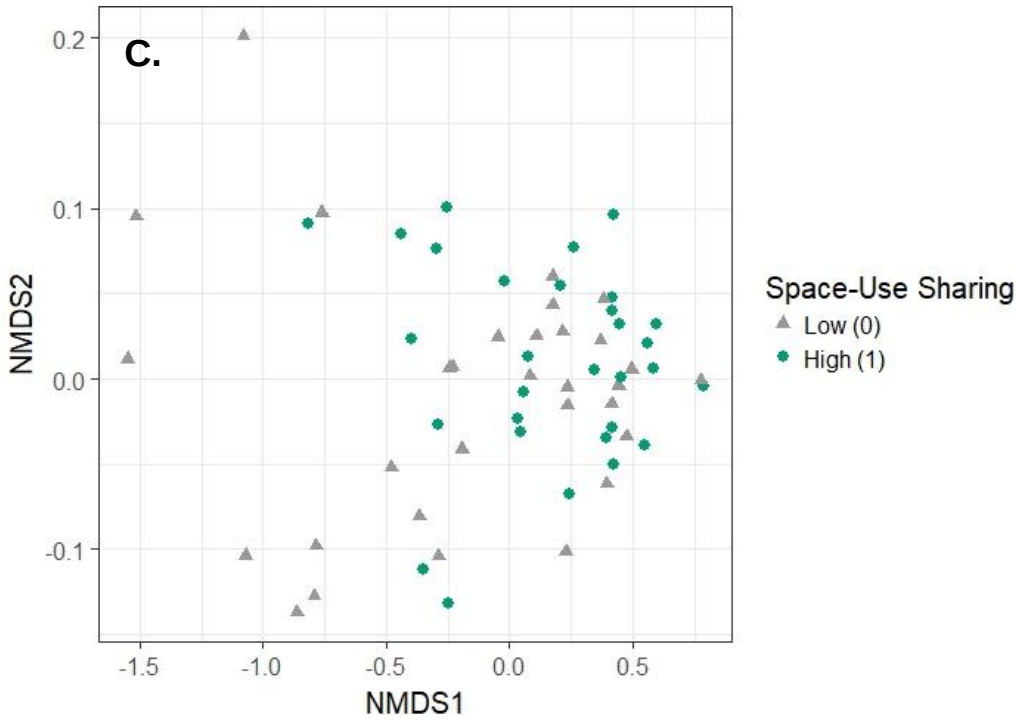
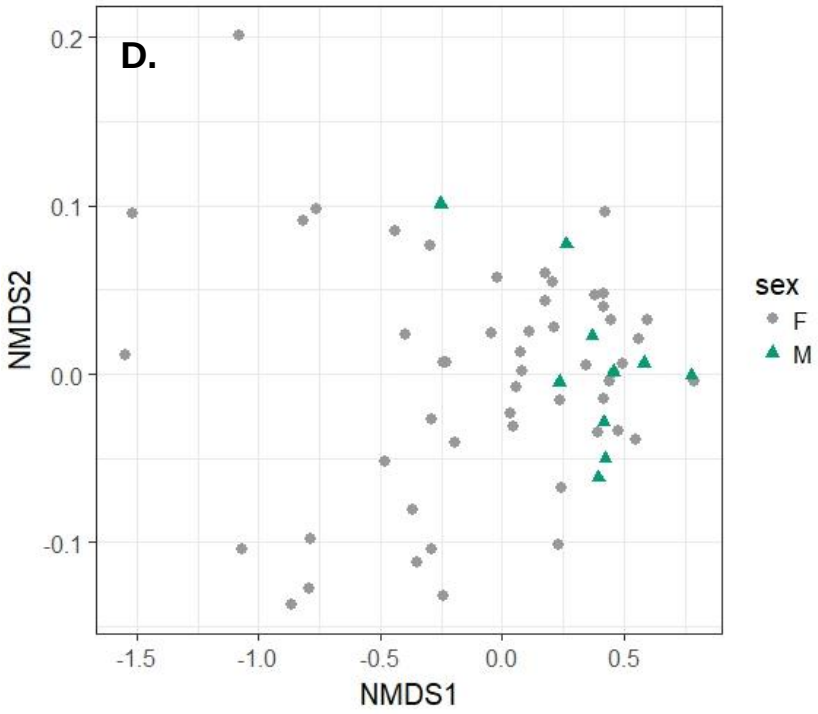


Figure 5. *Observations plotted by non-numeric variables on NMDS axes*. Observations are plotted as NMDS coordinates calculated based on similarity in the two clustering variables (daily path length, net daily displacement). Points are shaped and/or colored by values of non-numeric and binary variables, including: diffusion parameter (A.), turning direction (**B.**), space-use sharing (**C.**), sex (**D.**), and mortality status (**E.**). The lack of visible patterns on any plot suggests that differences between observations are not related to or caused by differences in values for these variables.




C.
0.2
0.1
0.0
-0.1
NMDS2
-1.5
-1.0
-0.5
0.0
0.5
NMDS1
Space-Use Sharing
Low (0)
High (1)


D.
0.2
0.1
0.0
-0.1
NMDS2
-1.5
-1.0
-0.5
0.0
0.5
NMDS1
sex
F
M

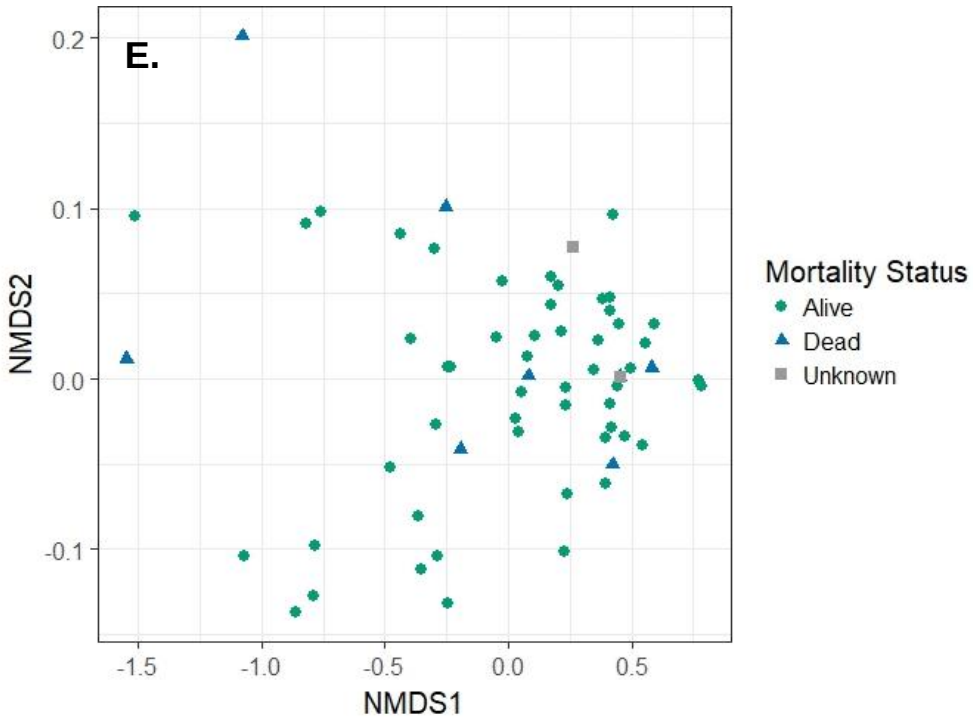
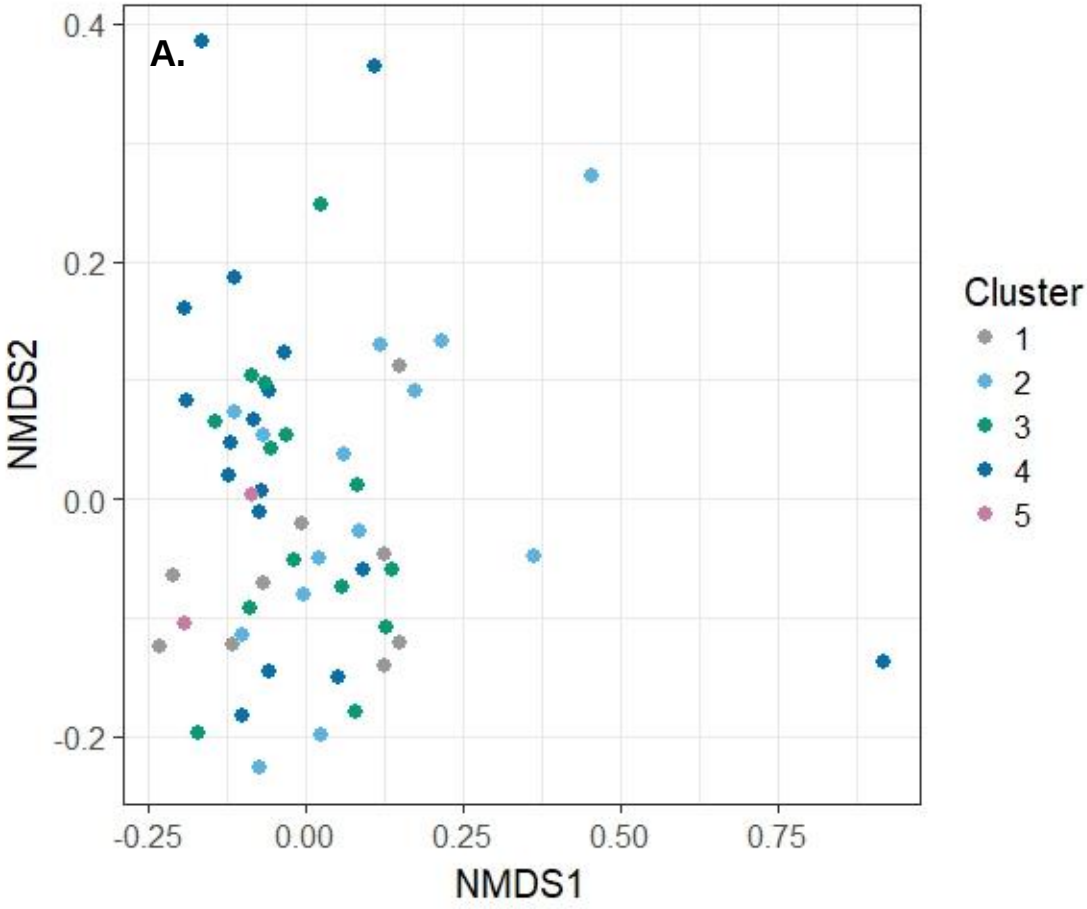

E.
0.2
0.1
0.0
-0.1
NMDS2
-1.5
-1.0
-0.5
0.0
0.5
NMDS1
Mortality Status
Alive
Dead
Unknown

Figure 6. *Winter observations plotted by two axes of environmental NMDS distances.* Observations are colored by cluster ID, as defined by k-means cluster analysis using the metrics daily path length and net daily displacement. Distances were calculated using all quantitative environmental variables. There does not appear to be any pattern in the arrangement of the observations with respect to cluster, suggesting that the differences between groups were not induced by environmental variables (**A.**). Values along NMDS2 were driven primarily by the proportion and patch area of deciduous forest and the proportion of mixed forest; values along NMDS1 were moderately driven by the proportion and edge density of coniferous forest (**B.**).



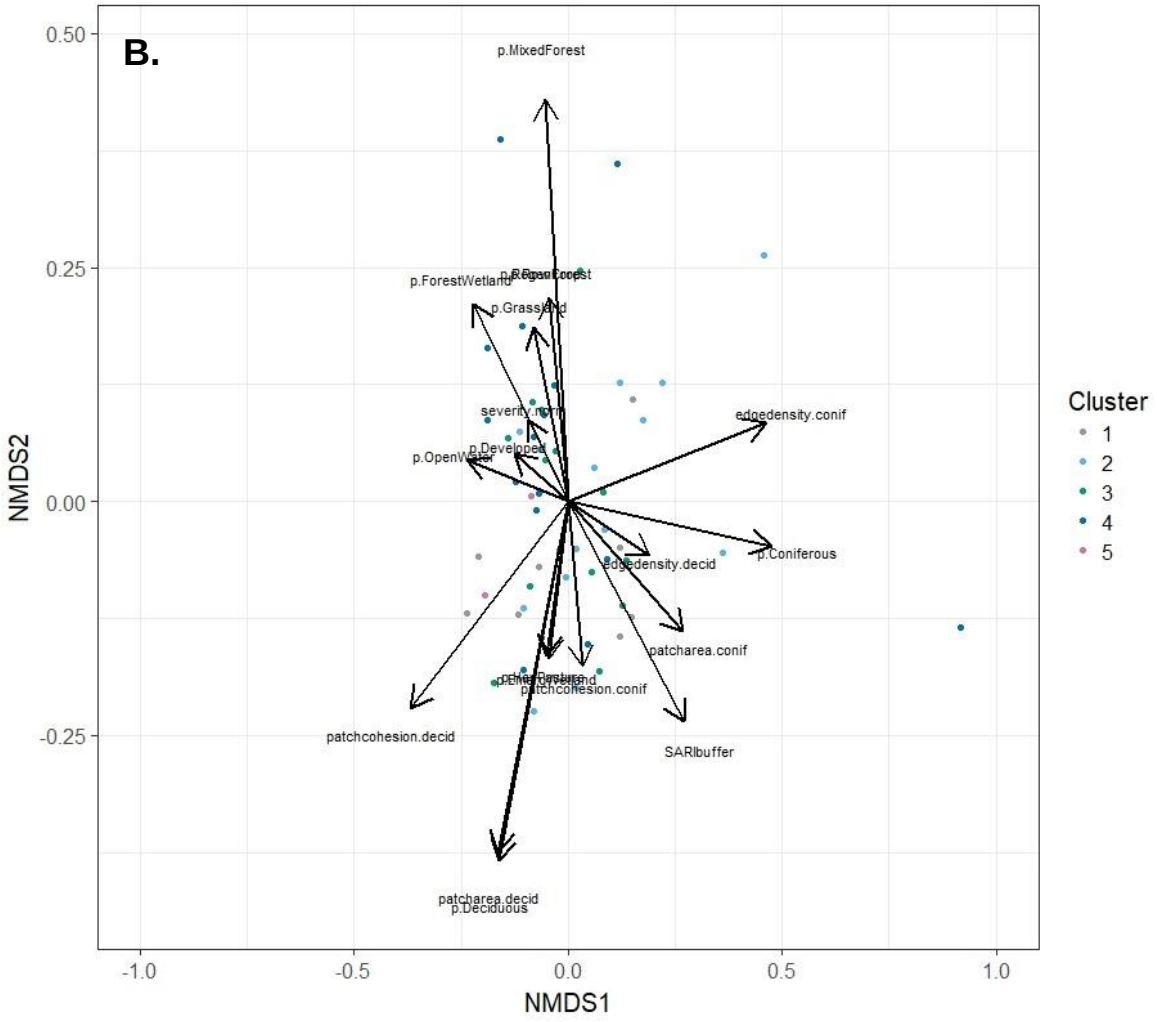
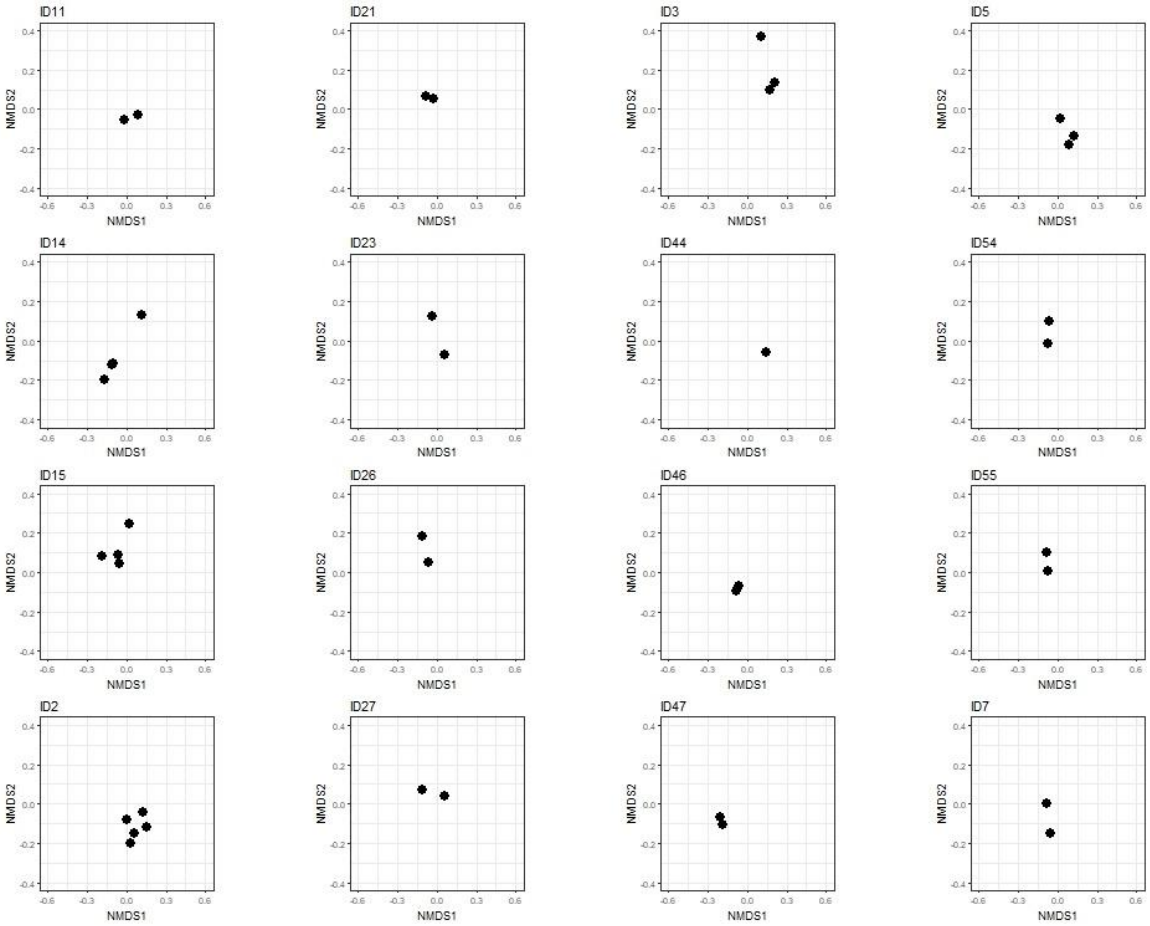

B.
p.MixedForest
p.ForestWetland
p.Grassland
severity.norm
p.Developped
p.OpenWater
edgedensity.conif
p.Coniferous
edgedensity.decid
patcharea.conif
patchcohesion.conif
patchcohesion.decid
SARIbuffer
patcharea.decid
p.Deciduous
0.50
0.25
0.00
-0.25
-1.0
-0.5
0.0
0.5
1.0
NMDS1
NMDS2
Cluster
1
2
3
4
5

Figure 7. *Similarity in environmental variables for individuals with more than one year of data.* Observations from individuals with more than one year of winter data were plotted on NMDS axes calculated using all continuous quantitative environmental variables. In the majority of cases, observations were more similar to each other than random, suggesting that individuals tended to be exposed to similar environmental conditions from year to year.



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Appendix 1. *Transformations applied to movement-derived behavioral metrics prior to cluster analysis*. Variables must be processed before they are inputted to a k-means cluster analysis. In the following table, "Metric" gives the abbreviation for the behavioral metric that was tested. "Season" is either "S" (summer) or "W" (winter); data from the two seasons were separated and inputted to two different cluster analyses. Outlies were identified as points outside 1.5 times the interquartile range above the upper quartile or below the lower quartile. "Outliers omitted" tells how many observations were identified as outliers and omitted from further analysis. If data were significantly skewed, the row text is bolded and the applied transformation is given under "Transformation." Distributions of variables were tested for normality using the Shapiro-Wilk test before and after transformation and outlier omission, if necessary; the final p-value is reported. In a final transformative step, all non-binary variables were normalized.

Metric	***Season***	***Outliers omitted***	***Transformation***	***Shapiro-Wilk p (post-transform)***
V	S	0	NA	0.064
V	W	1	NA	0.14
DPL	S	0	NA	0.45
DPL	W	1	NA	0.14
disp	S	0	NA	0.62
disp	**W**	**0**	**cube root**	**0.16**
D	S	2	NA	0.55
D	**W**	**7**	**binary**	**NA**
hr95	S	1	NA	0.62
hr95	**W**	**5**	**log**	**0.017**
angle score	S	NA	NA	NA
angle score	W	NA	NA	NA
kappa	S	NA	NA	NA
kappa	W	NA	NA	NA
SSmean	S	0	NA	0.059
SSmean	**W**	**many**	**binary**	**NA**
SARIdiff	S	NA	omit	NA
SARIdiff	W	NA	omit	NA
diff100	S	0	NA	0.15
diff100	W	1	NA	0.36
diff101	S	4	NA	0.94
diff101	W	4	NA	0.2
diff102	S	3	NA	0.75
diff102	W	1	NA	0.048
diff103	S	7	omit	NA
diff103	W	11	omit	NA
diff105	**S**	**0**	**binary**	**NA**
diff105	**W**	**3**	**binary**	**NA**
diff106	S	1	NA	0.17
diff106	W	0	NA	0.36
diff107	S	2	NA	0.96
diff107	W	3	NA	0.66
diff108	S	2	omit	NA
diff108	W	2	omit	NA
diff109	S	3	omit	NA
diff109	W	3	NA	0.16
diff110	S	4	omit	NA
diff110	W	6	omit	NA
diff111	S	NA	omit	NA
diff111	W	1	omit	NA

Appendix 2. *Results of mixed effects models for movement-derived behavioral metrics.* Mixed effects models were run to explain a response variable ("metric") by a fixed effect with or without interaction(s) and random effect(s). When seasons were assessed separately, the season is abbreviated in parentheses next to the metric name (e.g., "(W)"). For fixed effects that are factors, the value that corresponds to the coefficient estimate is abbreviated in parentheses next to the fixed effect. Models with coefficients significant at $\alpha = 0.05$ are bolded.

Metric	*Fixed Effect*	*Interaction*	*Random Effect(s)*	*Coefficient Estimate*	*t*	*p*
Velocity	**season (W)**	**NA**	**sex, ID**	**-32.51**	**-12.15**	**< 2e-16**
Velocity (W)	**sex (M)**	**NA**	**ID**	**8.121**	**2.178**	**0.0331**
Velocity (S)	sex (M)	NA	ID	0.247	0.023	0.982
Velocity	**mort (D)**	**season**	**sex, ID**	**-26.691**	**-2.811**	**0.00601**
Velocity	SARI	NA	sex, ID	-4.225	-0.593	0.555
DPL	**season (W)**	**NA**	**sex, ID**	**-778.19**	**-12.23**	**< 2e-16**
DPL (W)	**sex (M)**	**NA**	**ID**	**187.74**	**2.097**	**0.0399**
DPL (S)	sex (M)	NA	ID	9.721	0.038	0.97
DPL	**mort (D)**	**season**	**sex, ID**	**-372.49**	**-2.408**	**0.018**
DPL	SARI	NA	sex, ID	-96.45	-0.566	0.573
disp	**season (W)**	**NA**	**sex, ID**	**-353.35**	**-9.664**	**2.6e-14**
disp (W)	**sex (M)**	**NA**	**ID**	**158.58**	**2.835**	**0.00687**
disp (S)	sex (M)	NA	ID	-15.55	-0.116	0.908
disp	**mort (D)**	**season**	**sex, ID**	**-168.09**	**-2.073**	**0.041**
disp	SARI	NA	sex, ID	-111.89	-1.274	0.206
D	**season (W)**	**NA**	**sex, ID**	**-0.636**	**-4.568**	**2.06e-5**
D (W)	sex (M)	NA	ID	0.03290	0.171	0.865
D (S)	sex (M)	NA	ID	-0.1389	-0.185	0.8543
D	mort (D)	season	sex, ID	-0.4180	-1.561	0.122
D	SARI	NA	sex, ID	-0.08604	-0.289	0.7732
hr95	**season (W)**	**NA**	**sex, ID**	**-2.653**	**-5.948**	**9.51e-8**
hr95 (W)	sex (M)	NA	ID	0.3730	0.464	0.644
hr95 (S)	sex (M)	NA	ID	-0.8045	-0.544	0.59
hr95	**mort (D)**	**season**	**sex, ID**	**-1.7714**	**-2.109**	**0.0376**
hr95	SARI	NA	sex, ID	-1.4305	-1.558	0.123
hr95	severity	season	sex, ID	0.4640	0.502	0.617
hr95	patch area 106	NA	sex, ID	3.938e-5	0.030	0.976
hr95	edge density 106	NA	sex, ID	7.554	0.037	0.970
hr95	patch cohesion 106	NA	sex, ID	-0.5655	-0.284	0.777
hr95	patch area 105	NA	sex, ID	3.079e-4	0.170	0.866
hr95	edge density 105	NA	sex, ID	-73.781	-0.540	0.591
hr95	patch cohesion 105	NA	sex, ID	-2.348	-1.485	0.141
SSmean	season (W)	NA	sex, ID	-0.007083	-0.232	0.817
SSmean (W)	sex (M)	NA	ID	-0.005752	-0.102	0.919
SSmean (S)	sex (M)	NA	ID	-0.04495	-0.844	0.405
SSmean	severity	season	sex, ID	0.01163	0.211	0.8336
water	**season (W)**	**NA**	**sex, ID**	**-0.03765**	**-3.381**	**0.00136**
water (S)	mort (D)	NA	sex, ID	-0.06954	-1.855	0.0768